Canada

Fisheries and Oceans | Pêches et Océans

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Government of Canada
Fisheries and Oceans

Scientific Information
and Publications Branch
Ottawa K1A 0E6

Gouvernement du Canada
Pêches et Océans

Direction de l'information
et des publications scientifiques
Ottawa K1A 0E6

The *Canadian Journal of Fisheries and Aquatic Sciences* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, and *Journal of the Fisheries Research Board of Canada* 1938–79.

Editorial policy

The *Journal* publishes original research articles and notes, critical reviews, Perspectives (essays of opinion or hypothesis), comments, and book reviews. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmatory state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

It would assist the Editors if prospective authors identified briefly by covering letter (a) aspects of their papers that meet the foregoing objectives, (b) potential referees, and (c) other manuscripts contemplated or in press containing the same or similar information.

Submissions in English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. The use of proprietary names does not imply endorsement of the product or company.

A charge is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted.

Guides

Guides for authors and typists appear in the first issue of each volume and are available free from the *Journal*.

Subscriptions

The *Journal* is issued monthly to form annual volumes of twelve numbers and Supplements. Orders and inquiries regarding subscriptions must be sent directly to Supply and Serivces Canada, Ottawa, Ontario, Canada K1A 0S9. Prepayment is required in Canadian funds to the order of "The Receiver General for Canada."

Microfilm

Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Design: Ludvic Saleh & Associates, Ottawa

Conception graphique: Ludvic Saleh & Associates, Ottawa

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–79.

Politique de rédaction

Le *Journal* publie des articles et des notes fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (Perspectives), des commentaires et des comptes rendus de livres. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influencent les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus que corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles.

Les auteurs éventuels aideraient les rédacteurs s'ils identifiaient brièvement, dans une lettre d'accompagnement (a) les aspects de leurs textes qui répondent particulièrement aux objectifs indiqués ci-dessus, (b) des arbitres possibles et (c) d'autres manuscrits envisagés ou sous presse, dont la teneur est identique ou se rapproche de celui qui est soumis.

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le *Journal* décline toute responsabilité quant aux énoncés des contributeurs. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

Les manuscrits acceptés sont sujets à des frais de publication. Quant un auteur présente un texte, il doit préciser que ces frais seront acceptés. On trouvera dans une récente livraison du *Journal* les taux par page en vigueur.

Guides

Le guide des auteurs et celui des secrétaires d'auteurs paraissent dans la première livraison de chaque volume et sont disponibles gratuitement du *Journal*.

Abonnement

Le *Journal* paraît tous les mois, formant ainsi un volume de douze numéros et Supplements par année. On est prié d'adresser directement commandes et demande de renseignements relatifs à l'abonnement à Approvisionnements et Services Canada, Ottawa (Ontario), Canada K1A 0S9. Les paiements doivent être faits à l'avance en devises canadiennes, à l'ordre du « Receveur général du Canada ».

Microfilms

On peut acheter sur microfilms de 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, É.-U.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 43, No. 2, February 1986 **Volume 43, n° 2, février 1986**

Scientific Information and Publications Branch / Direction de l'information et des publications scientifiques

J. Watson, Ph.D. — *Director and Editor-in-Chief / Directeur et rédacteur en chef*
Johanna M. Reinhart, M.Sc. — *Deputy Director and Editor / Sous-directrice et rédactrice*
D. G. Cook, Ph.D. / Lorraine C. Smith, Ph.D. — *Assistant Editors / Rédacteurs adjoints*
J. Camp / G. J. Neville / P. M. Burke / M. L. Gilbert — *Editorial and Publishing Services / Services de rédaction et d'edition*
R. O. Brinkhurst, Ph.D. / J. R. M. Kelso, Ph.D. — *Book Review Editors / Rédacteurs des comptes rendus*

Editorial Board / Conseil de rédaction

L. Legendre	*Université Laval*	(1983–1986)
M. Sinclair	*Department of Fisheries and Oceans, Halifax*	(1983–1986)
C. J. Walters	*University of British Columbia*	(1983–1986)
C. M. Wood	*McMaster University*	(1983–1986)
P. J. Dillon	*Ontario Ministry of the Environment*	(1984–1987)
M. C. Healey	*Department of Fisheries and Oceans, Nanaimo*	(1984–1987)
J. J. Magnuson	*University of Wisconsin*	(1984–1987)
J. Sprague	*University of Guelph*	(1984–1987)
L. M. Dickie	*Department of Fisheries and Oceans, Dartmouth*	(1985–1988)
J. J. Dodson	*Université Laval*	(1985–1988)
S. J. Smith	*Department of Fisheries and Oceans, Dartmouth*	(1985–1988)
A. P. Zimmerman	*University of Toronto*	(1985–1988)

Editorial Office:
Scientific Information
and Publications Branch
Department of Fisheries and Oceans
Centennial Towers
200 Kent Street
Ottawa, Canada K1A 0E6

Bureau de rédaction :
Direction de l'information
et des publications scientifiques
Ministère des Pêches et des Océans
Les Tours Centennial
200, rue Kent
Ottawa, Canada K1A 0E6

The *Journal* is abstracted or indexed in: / Le *Journal* est résumé ou signalé dans :

Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, and Science Citation Index

Comparative Developmental Biology of Chum Salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia

Terry D. Beacham and Clyde B. Murray

Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6

Beacham, T. D., and C. B. Murray. 1986. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 43: 252–262.

Eggs and alevins from 32 families of chum salmon (*Oncorhynchus keta*) from seven Fraser River stocks spawning at different times or in different tributaries were incubated in controlled water temperatures of 4, 8, and 12°C. There were significant differences in egg and alevin survival among stocks and among families within stocks in the different incubation temperatures. Highest egg survival for a late-spawning Vedder River stock occurred at 4°C, while egg survival from other stocks was highest at 8°C. Late-spawning stocks had smaller eggs and earlier times of fry emergence than did early-spawning ones. There was no effect of spawning time on alevin hatching time. Alevins hatching at 8°C were larger than those hatching at 4 or 12°C, but there were no stock differences in alevin length or tissue weight. Stocks with greater egg sizes produced alevins of greater total weight. Fry emerging at 8°C were larger than those emerging at 4 or 12°C, and fry from early-spawning stocks were longer and had greater tissue weight than those from late-spawning ones. There were significant differences among families within stocks in size of alevins and fry, and family differences should be accounted for in studies of salmonid developmental biology.

Des oeufs et des alevins vésiculés de 32 familles de sept stocks de saumon kéta (*Oncorhynchus keta*) du fleuve Fraser frayant à des moments ou dans des tributaires différents ont été incubés ou placés dans des eaux dont la température était maintenue à 4, 8 ou 12°C. On a noté des différences significatives de la survie des oeufs et des alevins vésiculés entre les stocks et entre les familles au sein des stocks, en fonction de la température. La température permettant le taux de survie le plus élevé des oeufs était de 4°C pour un stock de la rivière Vedder frayant tard, mais de 8°C pour les autres stocks. Comparativement aux stocks frayant tôt, les stocks frayant tard avaient des oeufs plus petits et une émergence plus rapide des alevins non vésiculés. Le moment du frai n'avait aucun effet sur le moment de l'éclosion. L'éclosion à 8°C produisait des alevins plus gros que celle à 4 ou 12°C, mais la longueur et le poids des tissus des alevins vésiculés ne différaient pas entre les stocks. Le poids total des alevins vésiculés des stocks à oeufs plus gros était plus élevé, et les alevins non vésiculés ayant émergé à la température de 8°C étaient aussi plus gros que ceux ayant émergé aux autres températures. Les alevins non vésiculés des stocks frayant hâtivement étaient plus longs et présentaient une plus grande masse tissulaire que ceux des stocks à frai plus tardif. La taille des alevins vésiculés et non vésiculés présentait des différences significatives entre les familles d'un même stock, et ces différences devraient être prises en considération au cours des études portant sur la biologie du développement des salmonidés.

Received February 4, 1985
Accepted October 8, 1985
(J8103)

Reçu le 4 février 1985
Accepté le 8 octobre 1985

Chum salmon (*Oncorhynchus keta*) spawning in the Fraser River and its tributaries in southern British Columbia choose a variety of habitats, ranging from small creeks only a few kilometres in length to the mainstream Fraser River. The spawning period ranges from September through January, with the early-spawning stocks composed of larger, older fish than the late-spawning ones (Beacham 1984). Although the duration of the spawning season may range from 4 to 5 mo, the timing of downstream migration of fry in the spring usually occurs during a 6-wk period from mid-March to the end of April (Beacham and Starr 1982). Chum salmon stocks in the Fraser River are adapted in body shape to their natal river size (Beacham 1984). Differences among the stocks in timing of spawning and similarities in timing of fry migration suggest that the stocks may be adapted to their characteristic timing of spawning. Timing of spawning migration of the major Fraser River stocks has been summarized by Anderson and Beacham (1983).

Chum salmon stocks in which the adults spawn at different times but the fry migrate downstream at similar times may differ in the rate of development of the embryo from fertilization to hatching, and thus, given the same environmental conditions, alevins will hatch at different times. They may also differ in the length of time after hatching that the alevin resides in the gravel. Early- and late-spawning stocks may differ in one or both of these characteristics.

Studies on developmental biology of salmonids have used two basic experimental techniques. The first has been to cross a single male with a single female and assume that this family is representative of the stock or species in question (Hamor and Garside 1977; Peterson et al. 1977; Murray 1980; Heggberget and Wallace 1984). The second has been to pool both eggs and

TABLE 1. Collection dates in 1983 of gametes and surface water temperature (°C) at spawning time for chum salmon from four Fraser River tributaries.

Stock	Date	Temperature
Jones Creek	October 13	8.5
Alouette River	October 18	10.0
Vedder River	October 20 (early)	10.5
	October 28 (middle)	10.5
	November 28 (late)	5.0
Chehalis River	October 20 (early)	10.5
	December 19 (late)	1.0

sperm, sometimes from an unknown number of adults, and assume that a representative sample has been obtained (Hayes et al. 1953; Combs and Burrows 1957; Bailey and Evans 1971; Timoshina 1972; Gunnes 1979; Heming 1982; Wallace and Aasjord 1984). This has the disadvantage of ignoring family variation for the characters examined.

In our study, we examined whether or not variation in developmental biology of Fraser River chum salmon may be adaptive relative to timing of spawning. We also compared the variation in biological characters among stocks to the variation among families within stocks.

Materials and Methods

Gametes were collected in 1983 from individual male and female chum salmon from four tributaries of the Fraser River; the specific locations of the tributaries were outlined by Beacham and Murray (1985). Gametes were collected between October 13 and December 19 (Table 1). In this report, chum salmon spawning in the same river at different times are referred to as different stocks. For each stock, sperm from a single male fertilized the eggs of a single female, and from three to five families were obtained from each stock.

Eggs and sperm were transported to the laboratory on ice. Eggs were fertilized in the laboratory at 8°C, water-hardened, and reared at controlled temperatures of 4, 8, and 12°C. After water-hardening, 30 eggs from each female were preserved in 10% formalin for at least 90 d for subsequent determination of egg size. These eggs were then blotted dry and weighed to the nearest 1.0 mg on a top-loading electrobalance. The diameter of an egg was determined with Vernier calipers to the nearest 0.1 mm along the longest axis. Eggs were incubated in 10-tray vertical stack incubators, with each tray partitioned into 20 compartments by means of a removable plastic divider. Eggs from each family were divided into nine groups, with three groups, each in a different tray, assigned to each stack. Each of the families was thus replicated three times in each stack. The only exception was the early-spawning Vedder River stock, where, owing to the smaller number of eggs collected, families 1 and 2 had two replicates, and family 3 was represented by a single compartment in each stack. The trays were kept in darkness and were provided with a flow of dechlorinated Nanaimo tap water of 6.9 L/min. Oxygen concentrations were above 90% of air saturation at each temperature. Loading densities averaged about 4000 eggs/tray. This incubation environment was within the range of suitable conditions necessary for normal development (Bams and Simpson 1976). Water temperatures in each stack were recorded daily; and mean temperatures recorded for each stock under each controlled temperature regime are indicated in Table 2.

Dead eggs were removed from each compartment and stored in Stockard's solution (Rugh 1952). All dead eggs were inspected to determine which were unfertilized or the stage of development at which they died according to Vernier's (1969) classification. We recognized three stages of development: fertilization to epiboly (stage 17), epiboly to eye pigmentation (stage 25), and eye pigmentation to hatching (stage 30). Once hatching began in a compartment, we recorded the number of newly hatched alevins daily. Within 1 d of 50% hatching, 10 alevins from each compartment (30/family) were preserved in 10% formalin for subsequent determination of length and weights. After preservation for at least 90 d, alevins were blotted dry, and total (fork) length was measured to the nearest 0.1 mm. Total weight of the alevin was also recorded. The yolk was then separated from the rest of the body tissue and weighed. Tissue weight was then determined by subtraction. Dead alevins were removed from each compartment and the number recorded in order to determine survival rates from hatching to emergence of the fry.

We used an emergence trap (modified from Godin 1980) to determine timing of fry emergence. We constructed the trap from a Plexiglas aquarium bottom filter complete with lid and standpipe by placing a 4-cm layer of gravel in the bottom of the filter and fitting a layer of reinforced black plastic over the standpipe and the gravel. A 6-mm hole was cut in the plastic to enable fry to move out of the gravel when they emerged. These filters, each with its own air supply, were placed in 250-L tanks of water at the appropriate temperature. Thirty alevins from each family (10/replicate) were placed in the gravel when they were about two-thirds "buttoned-up" (late Vernier stage 35). The emergence traps were exposed to fluorescent light during the working day and natural light during the remainder of the day. The emergence traps were checked each afternoon for emergent fry. When 50% of the fry for a particular family had emerged, the remainder of the family in the stack was preserved in 10% formalin. After preservation for at least 90 d, 14 fry/replicate were unselectively drawn from the preserved sample and fry fork length, total weight, yolk weight, and tissue weight determined as for alevins.

Heterogeneity of survival rates among stocks and among families within stocks was tested by likelihood ratio (G-test) (Sokal and Rohlf 1969). The 50% hatching and emergence times were calculated using the method of Colby and Brooke (1969). Equality of alevin or fry length or weights among the replicates was tested by doubly nested analysis of variance using the following model (temperatures separate):

$$Y_{ijkl} = S_i + F_{ij} + R_{ijk} + e_{ijkl}$$

where Y = length or weight, S = stock ($i = 1, 7$), F = family within stock ($j = 1, 5$), R = replicate within family ($k = 1, 3$), and e = error term for the lth observation in subgroup ijk. All effects were considered random. Egg size differences among stocks and among families were tested by a similar model without the replicate term. Equality of alevin and fry lengths and weights among temperatures, stocks, and families was tested with the following model (all effects random):

$$Y_{ijkl} = T_i + S_j + TS_{ij} + F_{jk} + e_{ijkl}$$

where Y = length or weight, T = temperature ($i = 1, 3$), S = stock ($j = 1, 7$), TS = temperature and stock interaction, F =

TABLE 2. Survival rates of eggs and alevins for seven stocks of chum salmon incubated at
alevins and 50% emergence (days) of the fry is also indicated. Mean temperature (standard d
each stock is also recorded. *N* is the number of fertilized eggs (for egg survival rates) or alevi
emergence times are in parentheses.

			Egg				
			Survival				
Stock	Temperature	*N*	Fertilization to epiboly	Epiboly to eyed	Eyed to hatching	Fertilization to hatching	h
Jones	4.1 (0.25)	2409	0.93	1.00	0.99	0.91	123
	8.0 (0.24)	2094	0.97	1.00	0.97	0.94	68
	12.0 (0.27)	2029	0.96	1.00	0.94	0.91	45
Alouette	4.1 (0.26)	3488	0.91	1.00	0.96	0.88	121
	8.0 (0.23)	2758	0.99	1.00	0.99	0.99	68
	12.0 (0.22)	2804	0.94	1.00	0.90	0.84	45
Vedder							
Early	4.0 (0.24)	762	0.69	0.99	0.98	0.67	126
	8.0 (0.20)	910	0.94	1.00	0.97	0.91	69
	12.0 (0.19)	895	0.73	0.97	0.95	0.68	46
Middle	4.0 (0.23)	5264	0.97	1.00	1.00	0.96	126
	8.0 (0.19)	4726	1.00	1.00	1.00	0.99	69
	12.0 (0.16)	4883	0.93	0.99	0.98	0.89	45
Late	4.0 (0.19)	3086	0.97	0.98	0.99	0.94	125
	8.0 (0.16)	2824	0.92	0.99	0.99	0.90	67
	11.9 (0.22)	2983	0.88	0.97	0.95	0.81	46
Chehalis							
Early	4.1 (0.23)	3680	0.94	1.00	1.00	0.94	122
	8.0 (0.20)	3979	0.98	1.00	1.00	0.97	68
	12.0 (0.20)	4184	0.92	1.00	0.96	0.88	46
Late	4.0 (0.17)	3109	0.93	0.98	0.97	0.89	122
	8.0 (0.19)	3225	0.97	0.99	0.99	0.95	69
	12.0 (0.15)	2783	0.96	0.98	0.96	0.91	47

ubated at controlled temperatures of 4, 8, and 12°C. Time of 50% hatching (days) of the andard deviation in parentheses) observed under each controlled temperature regime for or alevins hatching (for alevin survival rates). Standard deviations of 50% hatching and

		Alevin				
				Survival		
on g	Time to 50% hatching	Temperature	N	Hatching to emergence	Fertilization to emergence	Time to 50% emergence
	123.0 (0.4)	4.0 (0.21)	2198	1.00	0.91	199.4 (2.7)
	68.0 (0.5)	8.0 (0.21)	1976	0.99	0.93	111.8 (0.8)
	45.3 (0.6)	12.0 (0.23)	1840	0.70	0.64	83.3 (2.0)
	121.8 (2.3)	4.0 (0.22)	3077	1.00	0.88	195.4 (5.7)
	68.6 (0.9)	8.0 (0.20)	2725	1.00	0.99	111.8 (1.6)
	45.4 (0.5)	12.0 (0.20)	2363	0.71	0.60	82.8 (1.3)
	126.5 (0.8)	4.0 (0.21)	510	1.00	0.67	198.4 (3.6)
	69.5 (0.1)	8.0 (0.19)	830	1.00	0.91	111.6 (0.9)
	46.3 (0.1)	12.0 (0.19)	606	0.94	0.64	84.4 (1.4)
	126.8 (1.4)	4.0 (0.21)	5075	1.00	0.96	200.9 (3.9)
	69.1 (0.5)	8.0 (0.21)	4665	1.00	0.99	106.1 (1.0)
	45.9 (0.4)	12.0 (0.18)	4367	0.87	0.77	77.5 (1.9)
	125.8 (1.2)	4.0 (0.18)	2915	1.00	0.94	188.4 (1.4)
	67.4 (0.6)	8.0 (0.18)	2549	1.00	0.90	104.4 (1.9)
	46.0 (0.6)	12.0 (0.20)	2429	0.97	0.79	72.0 (0.7)
	122.2 (2.2)	4.1 (0.21)	3449	1.00	0.94	196.8 (3.8)
	68.7 (0.7)	8.0 (0.19)	3868	1.00	0.97	111.7 (1.5)
	46.1 (0.5)	12.0 (0.19)	3679	0.82	0.72	84.8 (1.1)
	122.5 (1.8)	4.1 (0.43)	2768	1.00	0.89	182.7 (1.7)
	69.1 (0.7)	8.0 (0.17)	3060	0.97	0.92	102.1 (1.2)
	47.0 (0.8)	12.0 (0.14)	2531	0.78	0.71	64.8 (0.9)

TABLE 3. Likelihood ratio (G-test) for heterogeneity of survival rates of eggs and alevins for seven chum salmon stocks incubated at three controlled temperatures. $*P < 0.05$.

	Eggs		Alevins	
	df	G	df	G
12°C vs. 8°C	7	1466.4*	7	4187.8*
Jones	1	19.9*	1	756.6*
Alouette	1	440.3*	1	1062.2*
Vedder (early)	1	159.1*	1	27.7*
Vedder (middle)	1	415.5*	1	715.7*
Vedder (late)	1	93.5*	1	85.4*
Chehalis (early)	1	271.2*	1	1028.2*
Chehalis (late)	1	66.9*	1	512.0*
12°C vs. 4°C	7	623.5*	7	5028.1*
Jones	1	0.3	1	961.4*
Alouette	1	20.2*	1	1250.0*
Vedder (early)	1	0.1	1	43.6*
Vedder (middle)	1	192.6*	1	894.6*
Vedder (late)	1	251.1*	1	94.2*
Chehalis (early)	1	92.3*	1	986.5*
Chehalis (late)	1	66.9*	1	797.8*
8°C vs. 4° Jones	7	834.6*	7	124.6*
Jones	1	15.9*	1	20.4*
Alouette	1	313.9*	1	8.3*
Vedder (early)	1	156.0*	1	0.7
Vedder (middle)	1	57.5*	1	16.2*
Vedder (late)	1	35.6*	1	0.0
Chehalis (early)	1	44.5*	1	0.0
Chehalis (late)	1	211.2*	1	79.0*

family within stock ($k = 1, 5$), and e = error term for the lth observation in subgroup ijk.

Results

Survival

Survival of the eggs from fertilization to hatching was variable for the seven stocks examined. Survival rates varied from 67% for the early Vedder River eggs incubated at 4°C to 99% for the Alouette and middle Vedder River eggs incubated at 8°C (Table 2). Survival rates of the eggs incubated at 8°C were significantly higher than those incubated at 12 or 4°C for virtually all stocks (Table 3). The only exception was the late-spawning Vedder River stock, where eggs incubated at 4°C had a 94% survival rate compared with 90% rate for eggs incubated at 8°C ($P < 0.05$). In the late-spawning Vedder River stock, survival rates of the eggs declined as incubation temperature increased. Survival of eggs incubated at 4 and 12°C was similar for the Jones Creek and early-spawning Vedder River stock, but eggs incubated at 4°C had higher survival than those at 12°C for the Alouette River, middle- and late-spawning Vedder River stocks, and the early Chehalis River stock (Tables 2, 3).

Of those eggs incubated at 4°C that died, most of the mortality occurred during development from fertilization to epiboly (Table 2). This was consistent for all stocks incubated at 4°C. Of the eggs incubated at 12°C, the mortality of the Jones Creek and Alouette River stocks mostly occurred from eye pigmentation to hatching, whereas for the Vedder and Chehalis River stocks, most of the mortality occurred from fertilization to

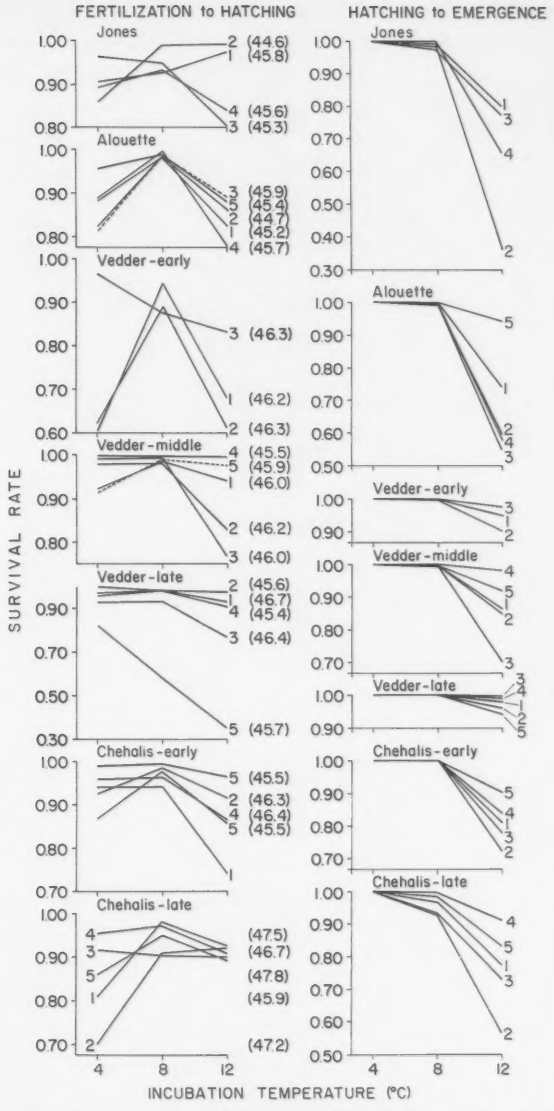


FIG. 1. Survival rates of eggs from fertilization to hatching and of alevins from hatching to emergence for 32 families from seven stocks of chum salmon. Families within stocks are numbered from 1 to 5. Time of 50% hatch (days) at an incubation temperature of 12°C is indicated in parentheses for each family.

epiboly (Table 2). Most of the mortality of eggs incubated in our study occurred during the early stages of development.

Survival of the alevins after hatching was virtually 100% for those eggs and alevins incubated at 4 and 8°C (Table 2). At 12°C, heavy alevin mortality occurred 1–3 d after hatching for most of the stocks examined. Those alevins that eventually died were characterized by sluggish movements, lack of head pigmentation, and eventual fungus infections of the gills. Alevins from the Jones Creek and Alouette River stocks, where egg survival from eye pigmentation to hatching was the lowest of the seven stocks surveyed, also had the lowest alevin survival.

TABLE 4. Likelihood ratio (G-test) for heterogeneity of survival rates of eggs and alevins among seven chum salmon stocks and among families within each stock. * $P < 0.05$.

	12°C				8°C				4°C				Total				Standardized measure	
	Eggs		Alevins		Eggs		Alevins		Eggs		Alevins		Eggs		Alevins			
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	df	G	Eggs	Alevins
Among stocks	6	410.1*	6	1077.9*	6	454.0*	6	258.2*	6	867.3*	6	27.0*	18	1731.4*	18	1363.1*	96.2	75.7
Within stocks	25	1774.2*	25	1201.5*	25	716.7*	25	99.6*	25	961.1*	25	7.2	75	3452.0*	75	1308.3*	46.0	17.4
Jones	3	164.0*	3	194.4*	3	21.9*	3	6.2	3	38.2*	3	4.2	9	224.1*	9	204.8*	24.9	22.8
Alouette	4	37.9*	4	343.9*	4	10.1*	4	12.0*	4	92.5*	4	0.0	12	140.5*	12	355.9*	11.7	30.4
Vedder (early)	2	26.0*	2	8.3*	2	10.6*	2	4.2	2	78.5*	2	0.0	6	115.1*	6	12.5	19.2	2.1
Vedder (middle)	4	465.6*	4	329.7*	4	10.1*	4	6.7	4	161.7*	4	0.0	12	637.4*	12	336.4*	53.1	28.0
Vedder (late)	4	886.9*	4	20.0*	4	558.6*	4	0.0	4	160.2*	4	0.0	12	1605.7*	12	20.0	133.8	1.7
Chehalis (early)	4	129.9*	4	108.3*	4	42.7*	4	0.0	4	116.0*	4	0.0	12	348.6*	12	108.3*	29.1	9.0
Chehalis (late)	4	3.9	4	196.9*	4	62.7*	4	70.5*	4	314.0*	4	3.0	12	380.6*	12	270.4*	31.7	22.5
Vedder																		
Early vs. middle	1	256.1*	1	22.8*	1	122.8*	1	0.0	1	553.6*	1	0.0	3	932.5*	3	22.8*	310.8	7.6
Early vs. late	1	70.7*	1	17.8*	1	0.6	1	3.7	1	291.9*	1	0.0	3	363.2*	3	21.5*	121.0	7.2
Middle vs. late	1	97.6*	1	232.2*	1	290.9*	1	8.5*	1	17.2*	1	0.0	3	405.7*	3	240.7*	135.2	80.2
Chehalis																		
Early vs. late	1	15.7*	1	14.5*	1	25.4*	1	155.4*	1	190.5*	1	0.0	3	231.6*	3	169.9*	77.2	56.6
Total	31	2184.3*	31	2279.4*	31	1170.7*	31	357.8*	31	1828.4*	31	34.2	93	5183.4*	93	2671.4*	55.7	28.7

At 12°C, alevins from the Vedder River had the highest survival of all stocks surveyed.

One objective of our study was to compare variation in biological characteristics among stocks with variation among families within stocks. Survival rates of eggs and alevins of different families within stocks could be markedly different (Fig. 1). At 4°C, survival rates of eggs from individual families ranged from 60 to 100% over all stocks. At 12°C, the difference in egg survival rates among families ranged from 35 to 100%. The variability in survival rates of eggs from different families within stocks was statistically significant in virtually all stocks at all temperatures (Table 4). The late-spawning Vedder River stock had the greatest heterogeneity in survival rates among families (Table 4), where at 12°C, one family had an overall egg survival of 35% and another had a 97% survival rate. The Alouette River stock had the least variation in egg survival rates among families (Table 4; Fig. 1).

We have demonstrated that families within stocks have heterogenous egg survival rates. On average, the differences in survival rates among stocks were greater than the differences among families within stocks ($F = 2.09$, df = 18,75, $P < 0.05$) (Table 4). Variability in survival rates among stocks relative to variation among families within stocks was greatest at 4°C ($F = 3.76$, df = 6,25, $P < 0.05$), significant at 8°C ($F = 2.63$, $P < 0.05$), but not significant at 12°C ($F = 0.96$, $P > 0.10$). At 12°C, heterogeneity in survival rates among families within stocks was just as large as the differences in survival rates among stocks. This was largely a result of the differences in survival rates of the middle- and late-spawning Vedder River families at 12°C (Table 4). Eggs from the middle-spawning Vedder River stock survived better than eggs from the early- and late-spawning stocks at all temperatures. Eggs from the late-spawning stock survived better than those from the early-spawning stock at 4 and 12°C. Eggs from the early-spawning Chehalis River stock survived better than those from the late-spawning stock at 4 and 8°C, but not at 12°C (Tables 2, 4).

Differences in alevin survival rates among stocks incubated at 12°C were greater than were egg survival rates (Table 4). Alevins from the Jones Creek and Alouette River stocks had the poorest survival (Table 2), but not all families within these stocks were affected equally (Fig. 1; Table 4). Heterogeneity in alevin survival rates among families at 12°C was greatest for the Jones, Alouette, and middle-spawning Vedder River stocks. In the Jones Creek stock, family 2, which had the highest egg survival at 12°C, had the lowest alevin survival, which indicates that mortality was delayed until after hatching in this instance. There was significant heterogeneity in alevin survival rates among families at 8°C for the Alouette and late-spawning Chehalis River stock, but alevins from all families within stocks survived equally well at 4°C (Table 4). Variability in alevin survival rates among stocks was greater than the variation among families with stocks at all incubation temperatures.

Hatching and Emergence Time

Hatching time of the alevins was similar for all stocks surveyed within each incubation temperature. Timing of spawning had no effect on hatching time of the alevins. The early-, middle-, and late-spawning stocks in the Vedder River all hatched at 46, 68–69, and 126–127 d at 12, 8, and 4°C, respectively (Table 2). The early- and late-spawning Chehalis

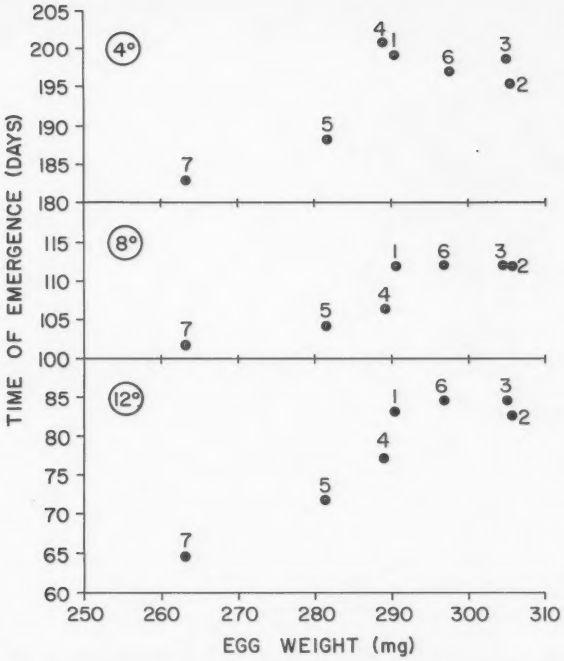


FIG. 2. Mean time of fry emergence from fertilization versus mean egg weight for seven stocks of chum salmon incubated at constant temperatures of 4, 8, and 12°C. Stocks: 1, Jones; 2, Alouette; 3, early Vedder; 4, middle Vedder; 5, late Vedder; 6, early Chehalis; 7, late Chehalis.

River stocks, separated in spawning time by 2 mo (Table 1), had alevins hatch at the same time when the same temperatures were compared. Any differences observed among stocks in hatching times were greatest at 4°C incubation temperatures. The Vedder River alevins all hatched between 126 and 127 d, but alevins from the other stocks hatched between 122 and 123 d. However, incubation temperatures for the Vedder River stocks were an average of 0.1° colder than the other stocks, and this probably accounts for the 3- to 4-d delay in hatching. Development rates of eggs from fertilization to hatching provide no evidence for stock adaptations of Fraser River chum salmon relative to their timing of spawning.

Emergence timing of the fry within each incubation temperature was dependent on the relative timing of spawning of the stock. Early-spawning stocks had heavier eggs ($F = 2.61$, df = 6,25, $P < 0.05$), and fry derived from these early-spawning stocks took longer to emerge from the gravel than did those from later-spawning ones (4°C, $F = 16.49$, $P < 0.01$; 8°C, $F = 41.82$, $P < 0.01$; 12°C, $F = 137.05$, $P < 0.01$) (Fig. 2). In the early-spawning Chehalis River stock, where mean egg weight was 298 mg, fry incubated at 12°C emerged after 85 d of incubation. In the late-spawning stock, where the mean egg weight was 263 mg, fry incubated at 12°C emerged 65 d after fertilization (Table 2). The Jones Creek, Alouette River, early-spawning Chehalis River, and early-spawning Vedder River stocks were all collected within a 1-wk interval (Table 1), and emergence timings of the fry of these stocks within each incubation temperature were very similar (Table 2). These early-spawning stocks also had the highest mean egg weights of the stocks surveyed. Although spawning time of chum salmon stocks in the Fraser River varies considerably, stock adaptations in egg size are such that fry from these stocks will emerge from the gravel redds at a similar time.

Alevin Size

Size of alevins at hatching was variable both among stocks within a single incubation temperature and among temperatures within a single stock (Table 5). Preliminary analysis indicated that there were no significant differences in alevin or fry length and weight among replicates within families ($P > 0.10$). Replicates for each family for each temperature were combined for further analysis. The analyses of variance indicated that there were significant differences in alevin fork length among families within stocks ($F = 13.07$, df = 25,2732, $P < 0.01$) and among incubation temperatures ($F = 5.54$, df = 2,12, $P < 0.05$), but no significant difference among stocks ($F = 1.62$, df = 6,18, $P > 0.05$). Alevins hatching at 8°C were longer than those hatching at 4 or 12°C, but there was no difference in alevin length between early- and late-spawning stocks. Analysis of variance of total alevin wet weight revealed significant differences among families within stocks ($F = 139.04$, $P < 0.01$), among incubation temperatures ($F = 13.21$, $P < 0.01$), and among stocks ($F = 8.22$, $P < 0.01$). Alevins hatching at 8°C were heavier than those hatching at other temperatures, and alevins from early-spawning stocks were heavier than those from late-spawning stocks (Table 5). Yolk weights of alevins hatching at 4°C were lower than those hatching at higher temperatures ($F = 7.15$, $P < 0.01$), and alevins from the early-spawning stocks with larger eggs had more yolk at hatching than did alevins from the late-spawning stocks ($F = 34.79$, $P < 0.01$) (Table 5). Alevin tissue weights showed the same trend as did fork lengths, being higher at 8°C than at the other incubation temperatures ($F = 7.79$, $P < 0.01$), but there were no differences among stocks ($F = 1.10$, $P > 0.05$). Significant variation occurred among families within stocks for all the alevin size characteristics investigated.

We examined the variation in alevin fork length and tissue weight among families within stocks. As with survival rates, families within stocks may show different trends in alevin length and tissue weight with respect to incubation temperature (Fig. 3). There were interactions between family and incubation temperature, so that families producing the smallest alevins at one incubation temperature may not necessarily produce the smallest alevins at another temperature. The magnitude of the family variance was only 12% of the magnitude of the stock variance for fork length, but 73% of the magnitude for total alevin weight, 62% for yolk weight, and 43% for tissue weight. Family variation clearly needs to be considered in analysis of trends in alevin size.

We examined variation in the developmental index K_D ($K_D = 10 \cdot$alevin or fry weight$^{0.333}$/alevin or fry fork length) (Bams 1970) in the same manner as the alevin size parameters. There were highly significant differences in this index among families within stocks ($F = 44.22$, df = 25,2732, $P < 0.01$) and among stocks ($F = 5.22$, df = 6,12, $P < 0.01$), but no significant differences among incubation temperatures ($F = 1.65$, $P > 0.05$). This index of development is clearly related to initial egg size, where alevins derived from families with larger initial egg sizes produce alevins with higher K_D values than other families in the same stock with smaller egg sizes (Fig. 4). Hatching times of the alevins from all families, regardless of their K_D values, were similar at each incubation temperature (Fig. 1). The early-spawning stocks with larger

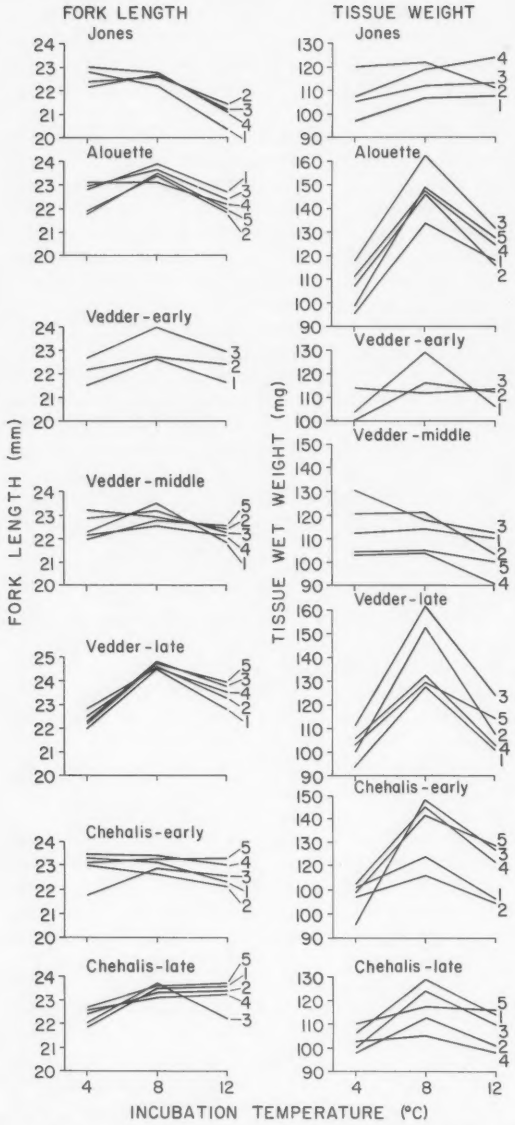


FIG. 3. Fork length and tissue weight of alevins at 50% hatching for 32 families from seven chum salmon stocks incubated at 4, 8, and 12°C.

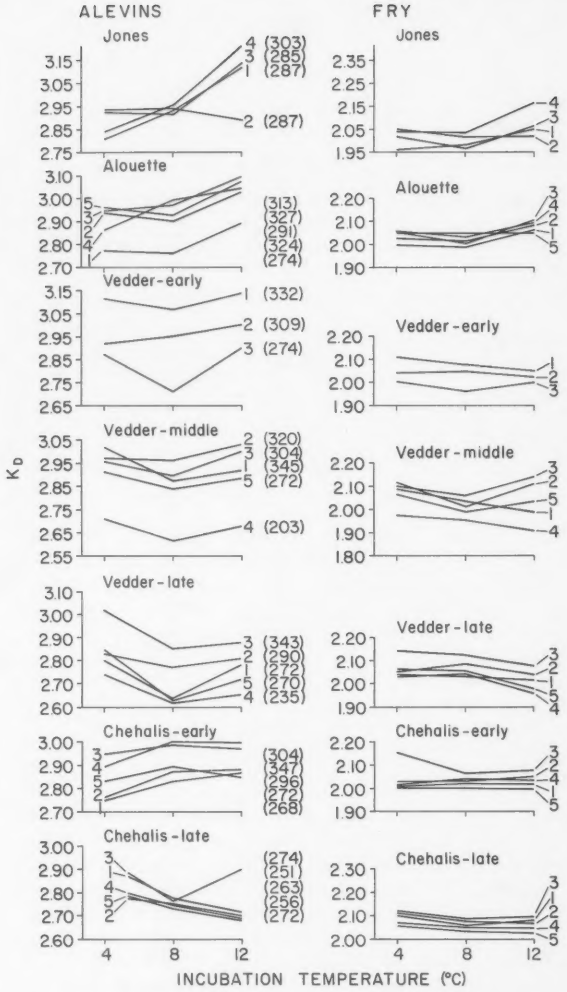


FIG. 4. K_D values (Bams 1970) for alevins at 50% hatch and fry at 50% emergence for 32 families of chum salmon incubated at 4, 8, and 12°C. Egg weights (mg) of each family are indicated in parentheses.

eggs produced alevins with higher K_D values than did the later-spawning stocks with smaller eggs. This index cannot be interpreted to decide whether alevins have hatched prematurely, as hatching times at 12°C were similar for all 32 families examined in our study (Fig. 1), yet the K_D values ranged from 2.68 to 3.19 (Fig. 4).

Fry Size

At emergence, there were significant differences in fry fork length among families within stocks ($F = 67.24$, df = 25,3820, $P < 0.01$), among incubation temperatures ($F = 8.02$, df = 2,12, $P < 0.01$), and among stocks ($F = 4.92$, df = 6,18, $P < 0.01$). As with alevins, the largest fry were produced at incubation temperatures of 8°C. Early-spawning stocks, having larger eggs than the late-spawning ones, also had longer fry at emergence. Similar results were found for fry total weight as for fork length, with families within stocks producing fry of unequal total weight ($F = 169.70$, $P < 0.01$), heavier fry produced at 8°C ($F = 4.55$, $P < 0.05$), and with early-spawning stocks producing heavier fry than late-spawning ones ($F = 4.55$, $P < 0.05$) (Table 5). Fry yolk weight at emergence varied among families within stocks ($F = 102.78$, $P < 0.01$) and among stocks ($F = 11.00$, $P < 0.01$), with fry from the middle-spawning Vedder River stock having the most yolk at emergence at all temperatures (Table 5). Fry emerging at the different incubation temperatures had similar amounts of yolk ($F = 219$, $P > 0.05$). Fry tissue weight had the same trends as fry total weight, as yolk weight at emergence usually comprised less than 10% of total

TABLE 5. Egg weight (mg) and diameter (mm), fork length (mm), total weight (mg
controlled temperatures (°C). *N* is the number of alevins and fry measured and wei

			Alevins			
Stock	Egg weight and diameter	Temperature	*N*	Fork length	Total weight	
Jones		4	120	22.6 (0.8)	276.5 (18.9)	
	290.4 (12.5)	8	119	22.5 (0.7)	288.8 (13.9)	
	8.4 (0.3)	12	115	21.0 (1.0)	286.6 (15.2)	
Alouette		4	150	22.5 (1.0)	276.0 (24.3)	
	305.6 (24.2)	8	144	23.5 (1.0)	317.9 (27.0)	
	8.6 (0.3)	12	149	22.3 (0.8)	302.3 (23.1)	
Vedder						
	Early	4	50	22.0 (0.7)	286.3 (21.7)	
	304.9 (26.8)	8	48	22.9 (0.9)	307.9 (26.7)	
	8.6 (0.3)	12	49	22.2 (0.9)	305.2 (15.0)	
	Middle	4	150	22.5 (1.1)	282.6 (45.3)	
	288.8 (50.3)	8	150	23.0 (0.7)	284.3 (43.8)	
	8.3 (0.5)	12	150	22.6 (1.0)	282.6 (41.0)	
	Late					
	281.9 (37.0)	4	150	22.4 (0.6)	260.8 (29.5)	
	8.2 (0.4)	8	149	24.6 (0.5)	295.9 (37.4)	
		12	150	23.4 (0.8)	272.6 (31.2)	
Chehalis						
	Early	4	150	22.9 (0.8)	274.4 (24.3)	
	297.5 (31.1)	8	148	23.1 (0.7)	306.6 (32.8)	
	8.5 (0.3)	12	150	22.7 (0.8)	288.8 (27.8)	
	Late	4	150	22.3 (0.6)	247.5 (16.0)	
	263.2 (12.3)	8	150	23.4 (0.6)	269.6 (17.4)	
	7.9 (0.4)	12	150	23.3 (1.3)	257.7 (19.0)	

eight (mg), yolk weight (mg), and tissue weight (mg) for chum salmon alevins and fry maintained at three and weighed for all families combined in each stock. Standard deviations are in parentheses.

Alevins			Fry				
t	Yolk weight	Tissue weight	*N*	Fork length	Total weight	Yolk weight	Tissue weight
8.9)	169.3 (8.2)	107.2 (16.5)	168	36.2 (0.8)	390.1 (21.6)	25.2 (9.1)	364.8 (22.3)
3.9)	173.8 (7.7)	115.1 (9.9)	168	38.0 (0.7)	437.0 (17.1)	17.1 (7.5)	419.8 (21.3)
5.2)	177.3 (13.9)	109.3 (10.3)	159	35.8 (1.1)	409.5 (32.9)	35.1 (11.2)	374.4 (34.2)
4.3)	170.3 (13.9)	105.6 (21.0)	210	35.9 (0.8)	394.1 (30.6)	34.2 (9.4)	359.9 (27.2)
7.0)	170.5 (13.0)	147.4 (18.1)	210	37.7 (0.9)	444.2 (23.7)	21.8 (8.6)	422.4 (19.8)
3.1)	178.6 (13.7)	123.7 (14.0)	210	36.3 (1.6)	427.7 (52.1)	33.4 (10.0)	394.2 (43.2)
1.7)	182.2 (17.7)	104.1 (12.0)	70	36.1 (1.2)	413.7 (32.8)	43.8 (17.4)	369.9 (30.2)
6.7)	187.0 (17.1)	120.9 (15.5)	66	36.8 (0.9)	422.6 (27.5)	39.9 (11.7)	382.7 (26.6)
5.0)	195.3 (12.8)	109.9 (13.2)	70	35.4 (1.3)	370.2 (29.7)	42.7 (14.2)	327.5 (34.5)
5.3)	168.4 (29.7)	114.2 (19.0)	210	35.3 (1.2)	392.9 (55.8)	54.0 (20.0)	338.9 (39.3)
3.8)	171.9 (30.9)	112.3 (18.8)	210	36.0 (1.2)	381.1 (51.7)	46.8 (18.5)	334.4 (39.7)
1.0)	179.0 (31.1)	103.6 (19.1)	210	33.0 (2.0)	307.8 (76.1)	62.4 (24.6)	245.4 (73.4)
9.5)	157.9 (22.8)	102.8 (14.0)	210	34.6 (0.9)	364.4 (36.7)	43.0 (14.8)	321.4 (27.3)
7.4)	155.2 (20.5)	140.7 (20.9)	210	34.9 (0.9)	374.7 (36.1)	42.9 (15.0)	331.8 (28.9)
1.2)	163.5 (19.4)	109.1 (17.5)	206	35.3 (1.0)	361.5 (37.8)	34.7 (18.3)	326.8 (39.4)
4.3)	167.6 (19.1)	106.8 (15.0)	210	36.0 (1.6)	397.3 (29.4)	20.1 (10.2)	377.1 (23.5)
2.8)	170.5 (19.6)	136.1 (18.9)	210	37.4 (1.1)	435.9 (31.0)	23.9 (10.0)	412.0 (24.8)
7.8)	171.3 (19.2)	117.5 (13.3)	195	35.9 (1.8)	395.7 (63.5)	29.3 (11.9)	366.3 (61.3)
6.0)	143.9 (10.6)	103.6 (13.2)	210	34.3 (0.7)	367.6 (16.8)	39.0 (14.0)	328.6 (20.3)
7.4)	152.0 (8.2)	117.6 (14.9)	200	35.2 (0.8)	383.4 (21.8)	35.7 (10.8)	347.6 (22.6)
9.0)	149.9 (12.5)	107.7 (25.6)	209	34.5 (0.7)	360.3 (17.6)	32.7 (9.7)	327.6 (20.1)

body weight. Fry from early-spawning stocks had greater tissue weight than those from late-spawning ones ($F = 6.81$, $P < 0.01$), and fry incubated at 8°C had the greatest tissue weight ($F = 5.30$, $P < 0.01$).

Variation in fry fork length and tissue weight among families within stocks was considerble (Fig. 5), accounting for the significant effect of families in the analyses of variance. Fry length and weight at 12°C were particularly variable among families in the middle-spawning Vedder River stock (Fig. 5). As with the alevins, there were interactions between family and incubation temperature. Family variation in fry length and weight is clearly a significant component of the total variance in these parameters.

At emergence, there were significant differences in the K_D values of fry from different families within stocks ($F = 44.32$, $P < 0.01$), but no differences among incubation temperatures ($F = 2.05$, $P > 0.05$) or stocks ($F = 0.95$, $P > 0.05$). The K_D values for most families varied between 1.95 and 2.15 (Fig. 4). Within a stock, fry from a family that had higher K_D values as alevins also had higher K_D values as emergent fry. The effect of initial egg size on fry K_D values was still apparent at emergence, although it was much reduced when compared with alevins (Fig. 4).

Discussion

Chum salmon spawning at different times vary in many biological characteristics (Smirnov 1975). In Asia, chum salmon are separated into summer and autumn seasonal races, and these races differ in size, spawning areas, fecundity, and age at maturity (Sano 1966). Similar biological differences exist between early and late runs of autumn-spawning chum salmon in Asia (Birman 1977) and in North America (Helle 1979; Beacham 1984). Variation in fecundity, age at maturity, and location of spawning among chum salmon stocks spawning at different times suggests that this variation is adaptive. Chum salmon return to their natal streams to spawn during a reasonably consistent period, and this homing implies that stocks of chum salmon are adapted to spawning during specific periods in their natal streams. As well as consistent homing to their natal streams, consistent timing of spawning migrations is a characteristic of returning Fraser River chum slamon (Anderson and Beacham 1983). Beacham (1984) demonstrated that chum salmon in southern British Columbia are modified in body shape to water flow conditions in their natal streams, indicating that variation in body shape is adaptive. Variation in biological characteristics among chum salmon stocks spawning at different times may suggest that the variation is adaptive.

Our study indicates that egg size differs between early- and late-spawning Fraser River chum salmon and that many differences in developmental biology are a consequence of this egg size difference. Early-spawning Fraser River chum salmon stocks are composed of more larger, older fish than are late-spawning ones (Beacham 1984), and as larger chum salmon usually have larger eggs than smaller ones (Watanabe 1955), differences in egg size between early- and late-spawning stocks are to be expected. Egg size has no effect on hatching time of alevins, but it has a considerable effect on emergence time of the fry. Variation in egg size appears to be a major mechanism by which fry emergence timing is regulated. It may also be regulated by differences in microhabitat selection by chum salmon spawning at different times. Initial egg size was also a determinant of fry size at emergence, with larger eggs producing larger fry. Similar observations have been made for a number of salmonid species (Yastrebkov 1966; Mead and Woodall 1968; Kazakov 1981; Wallace and Aasjord 1984; Beacham et al. 1985). Initial egg size may also influence subsequent growth and survival of the fry (Bagenal 1969; Bilton 1971; Gall 1974). There can be considerable variation in egg size among families within a stock, so that fry growth and survival from different families may be affected differentially.

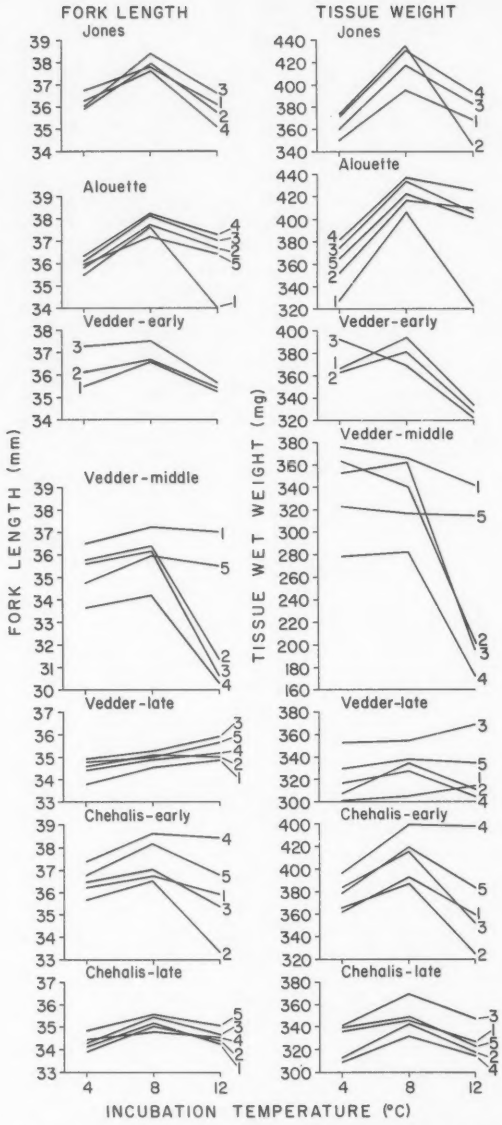


FIG. 5. Fork length and tissue weight of fry at 50% emergence for 32 families from seven chum salmon stocks incubated at 4, 8, and 12°C.

Differences in egg survival rates may be expected between early- and late-spawning stocks for eggs incubated under different temperature regimes. We expected that late-spawning stocks would have increased egg survival rates at low incubation temperatures and decreased rates at higher incubation tem-

peratures. Highest egg survival in the late-spawning Vedder River stock occurred at 4°C, but highest egg survival in the late-spawning Chehalis River stock occurred at 8°C. The Chehalis River, located near thermally active Harrison Hot Springs, has a significant groundwater input, and chum salmon spawn in these groundwater upwellings (Palmer 1972). Although surface water temperatures was 1°C at the time of spawning, groundwater temperature to which the eggs would be naturally exposed may be substantially higher. The Vedder River is not located in a thermally active area, and late-spawning chum salmon in the Vedder River may be adapted to lower water temperatures moreso than late-spawning chum salmon in the Chehalis River. Although there is some evidence to indicate that late-spawning Vedder River chum salmon were more adapted to cold water than were the other stocks, egg survival rates in our study were generally high. Incubation at threshold temperatures (Combs and Burrows 1957; Bailey and Evans 1971) may be necessary to investigate adaptive differences in egg survival rates for early- and late-spawning Fraser River chum salmon.

Maximum alevin and fry tissue weights occurred at an incubation temperature of 8°C, which suggests that the maximum efficiency of conversion of yolk to tissue weight is probably between 6 and 10°C for the chum salmon stocks in our survey. Maximum conversion efficiencies for brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) have been reported to be at 10°C (Marr 1966), that for chinook salmon (*Oncorhynchus tshawytscha*) at 6°C or below (Heming 1982), and that for chum salmon at 5°C or below (Murray 1980). However, Murray's study was based on a single family from one stock and may not be representative of general trends in chum salmon. For example, family 3 in the early-spawning Vedder River stock and family 1 in the middle-spawning Vedder River stock produced the heaviest fry at an incubation temperature of 4°C, similar to the results of Murray (1980), but our results indicate that this is not a general pattern for Fraser River chum salmon.

The K_D values (Bams 1970) of alevins at hatching have been interpreted as a measure to decide if alevins have hatched "prematurely" (Heming 1982). Heming interpreted a K_D value of 3.09 for chinook salmon alevins incubated at 12°C as evidence for premature hatching at that temperature, while K_D values for alevins incubated at lower temperatures ranged from 2.94 to 2.97. When our 32 families are considered, K_D values varied widely under each incubation temperature, but hatching times of the 32 families were similar (Fig. 1). Higher K_D values were not indicative of premature hatching in our study. Family 3 of the late-spawning Vedder River stock had a K_D value of 3.02 for alevins hatching at 4°C, while K_D values for the other families ranged between 2.74 and 2.84, but the alevins from family 3 hatched later than three other familes in the stock. Our results suggest that alevin K_D values are interpreted more appropriately as condition factors, rather than as an index of development.

Our study clearly illustrates that there is significant variation among families within stocks in egg and alevin survival and in alevin and fry size. If only one family per stock had been examined in our study, very different trends in the characteristics investigated could have resulted, depending on which family in the stock had been selected for study. Studies on salmonid developmental biology in which the results are based on a single family must be interpreted with caution. The other major approach in research on salmonid developmental biology has been to pool fertilized eggs from a number of parents. Variability in the characteristics investigated associated with families will not be accounted for, with the possibility that significant treatment effects will be found if the family effects are not examined in the experimental design.

In our study, we have examined stocks spawning only in Fraser River tributaries over a 2-mo period. A survey of stocks in the geographic and spawning time range of chum salmon in British Columbia may provide stronger evidence for adaptation of stocks to local environmental conditions. Also, investigation of the selection of spawning sites (i.e., groundwater sources) by different stocks may provide evidence for local adaptations to the environment.

Acknowledgments

Arthur Demsky, Eric Lauinger, Tim Netherall, and Karen Shillington weighed and measured the chum salmon eggs, alevins, and fry examined in this study, and also determined the stage of development of the eggs that died. Bruce Bernard assisted greatly in most of the data analysis. Lauri Mackie drafted the figures. The assistance of the staff at the Chehalis River and Chilliwack River hatcheries is also greatly appreciated. Drs. E. T. Garside and J. H. Helle provided many suggestions for improvement to the manuscript.

References

ANDERSON, A. D., AND T. D. BEACHAM. 1983. The migration and exploitation of chum salmon stocks of the Johnstone Strait – Fraser River Study Area, 1962–1970. Can. Tech. Rep. Fish. Aquat. Sci. 1166: 125 p.

BAGENAL, T. B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. J. Fish Biol., 1: 349–353.

BAILEY, J. E., AND D. R. EVANS. 1971. The low-temperature threshold for pink salmon eggs in relation to a proposed hydroelectric installation. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 69: 587–593.

BAMS, R. A. 1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish Res. Board Can. 27: 1429–1452.

BAMS, R. A., AND K. S. SIMPSON. 1976. Substrate incubator workshop — 1976. Report on current state-of-the-art. Fish Mar. Serv. Res. Div. Tech. Rep. 689: 67 p.

BEACHAM, T. D. 1984. Age and morphology of chum salmon (*Oncorhynchus keta*) in southern British Columbia. Trans. Am. Fish. Soc. 113: 727–736.

BEACHAM, T. D., AND C. B. MURRAY. 1985. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 312–319.

BEACHAM, T. D., AND P. STARR. 1982. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 80: 813–825.

BEACHAM, T. D., F. C. WITHLER, AND R. B. MORLEY. 1985. Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*O. kisutch*). Can. J. Zool. 63: 847–850.

BILTON, H. T. 1971. A hypothesis of alteration of age of return in successive generations of Skeena River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28: 513–516.

BIRMAN, I. B. 1977. Intrapopulation groupings of the Amur autumn chum salmon, *Oncorhynchus keta*. J. Ichthyol. 17: 741–750.

COLBY, P. J., AND L. T. BROOKE. 1969. Survival and development of lake herring (*Coregonus artedii*) eggs at various incubation temperatures. *In* C. C. Lindsey and C. G. Woods [ed.] Biology of Coregonid fishes. University of Manitoba Press, Winnipeg, Man. 392 p.

COMBS, B. D., AND R. E. BURROWS. 1957. Threshold temperatures for the normal development of chinook salmon eggs. Prog. Fish-Cult. 19: 3–6.

GALL, G. A. E. 1974. Influence of size of eggs and age of female on hatchability and growth in rainbow trout. Calif. Fish Game 60: 26–35.

GODIN, J.-G. J. 1980. Temporal aspects of juvenile pink salmon (*Oncorhynchus gorbuscha* Walbaum) emergence from a simulated gravel redd. Can. J. Zool. 58: 735–744.

GUNNES, K. 1979. Survival and development of Atlantic salmon eggs and fry at three different temperatures. Aquaculture 16: 211–218.

HAMOR, T., AND E. T. GARSIDE. 1977. Size relations and yolk utilization in embryonated ova and alevins of Atlantic salmon *Salmo salar* L. in various combinations of temperature and dissolved oxygen. Can. J. Zool. 55:

1892–1898.

HAYES, F. R., D. PELLUET, AND E. GORHAM. 1953. Some effects of temperature on the embryonic development of the salmon (*Salmo salar*). Can. J. Zool. 31: 42–51.

HEGGBERGET, T. G., AND J. C. WALLACE. 1984. Incubation of the eggs of Atlantic salmon, *Salmo salar*, at low temperatures. Can. J. Fish. Aquat. Sci. 41: 389–391.

HELLE, J. H. 1979. Influence of marine environment on age and size at maturity, growth and abundance of chum salmon, *Oncorhynchus keta* (*Walbaum*), from Olsen Creek, Prince William Sound, Alaska. Doctoral dissertation, Oregon State University, Corvallis, OR. 129 p.

HEMING, T. A. 1982. Effects of temperature on utilization of yolk by chinook salmon (*Oncorhynchus tshawytscha*) eggs and alevins. Can. J. Fish Aquat. Sci. 39: 184–190.

KAZAKOV, R. V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. J. Fish Biol. 19: 353–360.

MARR, D. H. A. 1966. Influence of temperature on the efficiency of growth of salmonid embryos. Nature (Lond.) 212(5065): 957–959.

MEAD, R. W., AND W. L. WOODALL. 1968. Comparison of sockeye salmon fry produced by hatcheries, artificial channels and natural spawning areas. Int. Pac. Salmon Fish. Comm. Prog. Rep. 20: 41 p.

MURRAY, C. B. 1980. Some effects of temperature on zygote and alevin survival, rate of development and size at hatching and emergence of Pacific salmon and rainbow trout. M.Sc. thesis, University of British Columbia, Vancouver, B.C. 156 p.

PALMER, R. N. 1972. Fraser River chum salmon. Can. Dep. Environ. Fish. Serv. Pac. Reg. Tech. Rep. 1972-1: 284 p.

PETERSON, R. H., H. C. E. SPINNEY, AND A. SREEDHARAN. 1977. Development of Atlantic salmon (*Salmo salar*) eggs and alevins under varied temperature regimes. J. Fish. Res. Board Can. 34: 31–43.

RUGH, R. 1952. Experimental embryology. Burgess Publishing Co., Minneapolis, MN. 480 p.

SANO, S. 1966. Salmon of the North Pacific Ocean. Part III. A review of the life history of North Pacific salmon. 3. Chum salmon in the Far East. Int. North Pac. Fish. Comm. Bull. 18: 41–57.

SMIRNOV, A. I. 1975. The biology, reproduction and development of the Pacific salmon. Izd. Mosk. Univ. 335 p. (Fish. Mar. Serv. Transl. Ser. No. 3861)

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman and Co., San Francisco, CA. 776 p.

TIMOSHINA, L. A. 1972. Embryonic development of the rainbow trout (*Salmo gairdneri*, *irideus* Gibb) at different temperatures. J. Ichthyol. 12 (3): 425–432.

VERNIER, J.-M. 1969. Chronological table of the embryonic development of rainbow trout. Ann. Embryol. Morphog. 2: 495–520. (Fish. Mar. Serv. Transl. Ser. No. 3913)

WALLACE, J. C., AND D. AASJORD. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). J. Fish Biol. 24: 427–435.

WATANABE, M. 1955. Some observations on the eggs of the mature salmon (*Oncorhynchus keta*) in Hokkaido, with special reference to the race of salmon as characterized by the size of their eggs. Sci. Rep. Hokkaido Fish. Hatch. 101: 7–20. (In Japanese, Engl. abstract).

YASTREBKOV, A. A. 1966. Effect of egg size upon size and growth rate of pink salmon larvae. Tr. Murmansk. Morsk. Biol. Inst. 12(16): 45–53. (Fish. Res. Board Transl. No. 1822)

Winter Survival and Growth of *Chondrus crispus* in Onshore Culture Tanks[1,2]

Peter F. Shacklock and James S. Craigie

Atlantic Research Laboratory, National Research Council of Canada, 1411 Oxford Street, Halifax, N.S. B3H 3Z1

Shacklock, P. F., and J. S. Craigie. 1986. Winter survival and growth of *Chondrus crispus* in onshore culture tanks. Can. J. Fish. Aquat. Sci. 43: 263–268.

Commercial aquaculture of *Chondrus crispus* in eastern Canada required the development of reliable methods for ensuring the winter survival of a healthy, vegetative inoculum. Two procedures were investigated. Agitated cultures of *C. crispus* (stocking density <6 $kg \cdot m^{-2}$) in running seawater grew at average rates of 0.21–0.34 $kg \cdot m^{-2} \cdot wk^{-1}$ during two winters under natural irradiance. Cultures maintained in undisturbed, outdoor tanks of seawater over three winters showed little or no net production; however, survival was excellent provided that the stocking density remained below approximately 10 $kg \cdot m^{-2}$. The plants were capable of resuming growth when environmental conditions improved. We found no difference in the responses of the several haploid and diploid isolates examined. Large vegetative inocula required for commercial aquaculture can be maintained simply and reliably in tanks of clean seawater if they are undisturbed and an ice cover is allowed to form.

L'aquiculture commerciale de *Chondrus crispus* dans l'est du Canada a nécessité la mise au point de méthodes fiables pour assurer la survie pendant l'hiver d'un inoculum végétatif sain. On a examiné deux procédures. Des cultures de *C. crispus* (densité de mise en charge <6 $kg \cdot m^{-2}$) placées dans de l'eau de mer courante se sont développées à des taux moyens variant de 0,21 à 0,34 $kg \cdot m^{-2} \cdot sem^{-1}$ pendant deux hivers sous une irradiation naturelle. Les cultures gardées dans des réservoirs extérieurs d'eau de mer non agités pendant ces deux hivers ont connu une production nette faible ou nulle; cependant, la survie s'est avérée excellente en autant que la densité de mise en charge ait été maintenue en-dessous de 10 $kg \cdot m^{-2}$ environ. Les plantes ont pu recommencer à croître lorsque les conditions environnementales se sont améliorées. Nous n'avons trouvé aucune différence dans les réactions des nombreux isolats haploïdes et diploïdes examinés. Les gros inoculums végétatifs nécessaires à l'aquiculture commerciale peuvent être gardés simplement et de façon sûre dans des réservoirs remplis d'eau de mer propre s'il n'y a pas d'agitation et si on laisse se former une couverture de glace.

Received April 17, 1985
Accepted October 16, 1985
(J8206)

Reçu le 17 avril 1985
Accepté le 16 octobre 1985

The red alga *Chondrus crispus* Stackhouse (Irish moss) has been harvested in the Canadian Maritimes for some 45 yr as a source of the commercially valuable phycocolloid, carrageenan. More recently, techniques have been developed to grow *C. crispus* in outdoor aquaculture facilities (Shacklock et al. 1975). To maintain the vegetative plants, we needed to develop a simple protocol for ensuring that an inoculum would survive the winter in a healthy condition and be capable of resuming rapid growth in the spring. Because it was anticipated that such an overwintering process would be conducted on a large scale, it should be efficient and cost effective. We report on experiments performed over five winters during which *C. crispus* was maintained in outdoor tanks either in a polyethylene-covered structure or in uncovered open tanks.

Materials and Methods

All experiments were conducted at the Fink Cove facility of the National Research Council of Canada (NRCC) near Halifax, N.S. (Neish et al. 1977). An initial overwintering experiment was conducted in 1972–73 in a 24.5-m^2 concrete tank housed in a clear polyethylene (15 mil) covered structure (Shacklock et al. 1975). For the present experiments, the original paddle systems were removed and the structure was used to house six 1.46-m^2 fiber glass tanks. For the winters of 1979–80 and 1980–81, the frame was recovered with new polyethylene; in all later experiments (1981–84), no polyethylene cover was used.

Three sizes of fiber glass tanks were employed: 1.46 m^2 (1.21 × 1.21 × 0.68 m high) and two of 2.88 m^2 (2.4 × 1.2 m and either 0.6 or 0.9 m high). The 0.6-m-high rectangular tanks were equipped for paddle agitation (Simpson et al. 1978). The remaining tanks were equipped for compressed air agitation of the plants and seawater. The exposed sides of all tanks used outside the polyethylene shelter were covered in November with polyurethane board of 2.5 cm thickness. When the water

[1]Issued as NRCC No. 24796.

[2]Presented at the Second Annual Aquaculture Association of Canada Meeting, Halifax, N.S., March 5–9, 1985, and Phycological Society of America, Gainesville, FL, August 13–15, 1985.

TABLE 1. Survival of *C. crispus* in outdoor, uncovered 2.88-m^2 tanks during 1980–81. Agitation (paddle type) and seawater supply were discontinued on December 12 and resumed on February 23.

Isolate	Initial stocking density ($kg \cdot m^{-2}$): Dec. 12	Biomass ($kg \cdot m^{-2}$)[a] Feb. 23	Apr. 3	Apr. 28	May 14	May 21	Mortality (% dead) Feb. 23[b]	Apr. 3[c]
T4	10.4	8.7	7.3	6.8	8.1	—	50	23.7
T4	22.6	—	—	4.6	5.8	—	90	65.3
ARL-16	8.5	8.1	7.4	—	—	9.4	10	2.8
750128C	8.3	7.0	6.1	—	—	9.3	20	3.7

[a]Biomass included both living and dead *C. crispus* on Feb. 23 and Apr. 3. On Apr. 28 and subsequently, no dead *C. crispus* were present.
[b]Mortality was estimated visually.
[c]Mortality was determined by sorting 100- to 500-g samples and weighing the live and dead plants.

temperature approached 0°C, before the freeze-up, the seawater and air delivery systems were disconnected and the overflow standpipes were removed and replaced by rubber stoppers to avoid potential water leaks. Finally, a 10- to 15-cm-diameter peeled spruce log was floated diagonally in each tank to accommodate the expansion pressure caused during ice formation.

The *C. crispus* was from cultures maintained at the Atlantic Research Laboratory, NRCC. The haploid isolates were T4 (Neish and Fox 1971; Neish et al. 1977; Guiry 1981), two green-colored mutants (T4G and T4dG) derived from the same stock, and a broad frond morphotype, BH-H, derived from isolates collected at Basin Head, P.E.I. The diploid plants tested were ARL-16 (Chen et al. 1982), 750128C (Chen et al. 1982), and a new isolate, NRCC-BH-D, with broad fronds. The latter originated from the germination of carpospores derived from Basin Head stock in June of 1982.

Supplemental nutrients were added only to cultures which were kept agitated in flowing seawater during the winter; a solution of commercial grade NH_4NO_3 and $(NH_4)_2HPO_4$ was added monthly to each tank to raise the nitrogen level to 1 m*M* and phosphate to 0.1 m*M*.

Growth and tank stocking densities were determined on a unit area basis, since plant growth is more closely related to the surface area of a tank rather than the volume (Shacklock et al. 1975). Plant weights were measured periodically by collecting the *C. crispus* in nylon mesh baskets (Nitex 16-1190). The baskets were suspended indoors at low temperature (<10°C) for 10 min to drain before recording the weight of the *C. crispus* on a spring scale (Toledo model 2110). The change in weight (kilograms) of a culture from one weighing to another, divided by the surface area of the tank (square metres), was called "net production." "Growth rate" is net production expressed per unit time (1 wk).

When grazers *Idotea balthica* (Pallas), *Gammarus oceanicus* (Segerstråle), and *Lacuna vincta* (Montagu) appeared to be abundant, insecticides were used to reduce or eliminate them (Shacklock and Croft 1981). Single batch applications of dimethoate (2.5 $mg \cdot L^{-1}$) for 12–24 h were sufficient to kill the crustaceans although second applications were made if *L. vincta* persisted.

Results

Figure 1 shows the performance of *C. crispus* isolates held during the winters of 1979–80 and 1980–81 in 1.46-m^2 tanks inside the unheated polyethylene-covered structure. Both aeration and a high flow (>10 tank volumes $\cdot d^{-1}$) of seawater were provided continuously. Plant stocking densities varied during the tests, but were kept below 6 $kg \cdot m^{-2}$ by removing excess biomass during the weighing procedures. In 1979–80 the growth rate was highest in November–December (0.55 ± 0.06 $kg \cdot m^{-2} \cdot wk^{-1}$, $n = 6$) and lowest in December–January (0.14 ± 0.04 $kg \cdot m^{-2} \cdot wk^{-1}$, $n = 6$). Growth improved in January–February (0.18 $kg \cdot m^{-2} \cdot wk^{-1}$, $n = 6$) and again in February –March (0.34 $kg \cdot m^{-2} \cdot wk^{-1}$, $n = 6$) although the temperature was at the minimum during the latter period. Analysis of variance showed that growth in the January–February period of each year was significantly ($p = 0.05$) greater than that in the corresponding December–January period. In 1980 the experiments were initiated in December, and again growth rates were lowest during the December–January interval and improved as the irradiance increased. Average growth rate (kilograms per square metre per week) for the isolates grown during 1979–80 ranged from 0.24 (T4dG) to 0.34 (T4G). The remaining isolates (T4, ARL-16, and 750128C) all produced 0.28 $kg \cdot m^{-2} \cdot wk^{-1}$. During the winter of 1980–81, T4 again produced an average of 0.28 $kg \cdot m^{-2} \cdot wk^{-1}$, while ARL-16 and 750128C produced 0.21 and 0.24 $kg \cdot m^{-2} \cdot wk^{-1}$, respectively.

When plants were left undisturbed at high stocking densities during the winter in unprotected outdoor tanks of seawater, damage occurred (Table 1). Mortality was severe at stocking densities >10 $kg \cdot m^{-2}$. Damage to the plants was apparently caused by their being frozen in the undersurface of the ice cover and by being buried deeply in unstirred mounds. Ice covered the tanks almost continuously from December 12 to February 20. On February 6, following 2 wk with an average daily mean air temperature of −6.6°C, the measured thickness of ice was 37 cm. When paddle agitation was resumed the dead fronds began to fragment and were gradually flushed from the tanks in the seawater overflow, thus accounting for the loss in biomass. The surviving *C. crispus* resumed normal growth.

During the winter of 1981–82, *C. crispus* survival was excellent when initial stocking densities were 8 $kg \cdot m^{-2}$ or less (Table 2). At a stocking density of 5 $kg \cdot m^{-2}$, net production was positive for both isolates. Most of this growth occurred before the agitation regime and seawater supply were interrupted (data not shown). The approximately fivefold difference in winter net production for the BH-H isolate apparently reflects the difference between air agitation (1.46-m^2 tanks) and paddle agitation (2.88-m^2 tanks), as the environmental condi-

TABLE 2. Net production in winter and subsequent growth rates of haploid *C. crispus* isolates overwintered in uncovered, outdoor tanks during 1981–82. O_2 was supplied to four tanks of isolate T4 when the agitation and seawater supply were discontinued.

Isolate	Stocking density ($kg \cdot m^{-2}$)	Tank size (m^2)	Nov. 25 – Mar. 30 net production ($kg \cdot m^{-2}$)[a]	Mortality (percentage of plants showing damage)[b]		Mar. 31 – Apr. 30 growth rate ($kg \cdot m^{-2} \cdot wk^{-1}$)[c]
				Apices only	Whole plant	
T4	5	1.46	+0.53	16.3	5.0	0.43
T4	5	1.46	+0.31	1.1	0	0.49
T4	8	1.46	−0.08	7.2	1.1	0.28
T4	11	1.46	−3.65	0	100	—
T4	11	1.46	−1.25	22.9	2.7	0.27
T4	14	1.46	−2.29	8.7	23.3	0.20
T4	14	1.46	−2.27	32.3	6.9	−0.13
T4+O_2	8	2.88[d]	−0.53	2.5	1.9	0.41
T4+O_2	11	1.46	−0.27	9.8	4.0	0.20
T4+O_2	14	1.46	−0.40	10.7	3.8	0.25
T4+O_2	14	2.88[d]	−1.79	5.0	2.2	0.29
BH−H	5	1.46	+0.70	0	0	0.37
BH−H	5	1.46	+0.74	0	0	0.33
BH−H	5	2.88[d]	+0.10	0	0	0.30
BH−H	5	2.88[d]	+0.16	0	0	0.29

[a]Agitation and seawater supply were discontinued Dec. 21 and resumed between Mar. 16 and 24.
[b]Determined on 100- to 300-g samples sorted on Apr. 6 into living and dead or injured plants.
[c]Stocking densities were kept below 8 $kg \cdot m^{-2}$.
[d]These tanks were paddle agitated between Nov. 25 and Dec. 21 and air agitated after Mar. 24.

tions were similar. During April, air agitation was used for both tank sizes and no obvious differences in growth rates were recorded.

Four tanks containing isolate T4 were supplied with a low flow of O_2 through a sparger. The addition of O_2 appeared to be beneficial at stocking densities of 11 and 14 $kg \cdot m^{-2}$, as injury to the alga was much less than in controls stocked at the same densities (Table 2). Significant injury to *C. crispus* occurred at loading densities of 11 and 14 $kg \cdot m^{-2}$ when O_2 was not supplied. In only one tank (T4 at 11 $kg \cdot m^{-2}$) was the *C. crispus* totally destroyed. The location of this tank was in the northwest corner of the site, and its more extreme exposure may have been a factor in causing the winter kill. A maximum depth of ice (35 cm in a 68-cm-deep tank) was recorded on February 2; salinities of 37–58‰ were measured in samples of the seawater taken from beneath the ice. The higher salinities occurred near the bottom of the tanks.

Experiments during 1982–84 (Table 3) confirmed our earlier observations (Tables 1, 2) that low stocking densities would permit virtually complete survival of both haploid and diploid isolates of *C. crispus*. The few dead plants found had floated and been trapped in the ice. At the higher stocking densities (10 $kg \cdot m^{-2}$), great year-to-year variability was noted with the complete loss of *C. crispus* in five of six tanks in 1982–83 and the almost complete survival of plants held under similar conditions in 1983–84. Some fronds showed orangish–pink regions indicating injury of undetermined origin, but perhaps associated with the higher stocking densities. After a recovery period, all surviving plants were capable of resuming growth as the environmental conditions improved (Table 3).

Discussion

Data for 1979–80 and 1980–81 establish that *C. crispus* can grow throughout the winter (Fig. 1). Shacklock et al. (1975) showed that between November 6, 1972, and February 28, 1973, the biomass of *C. crispus* increased from 71.8 kg (2.9 $kg \cdot m^{-2}$) to 120.6 kg (4.9 $kg \cdot m^{-2}$) for an average growth rate of 0.12 $kg \cdot m^{-2} \cdot wk^{-1}$. The seawater temperature ranged between +9 and −1°C during this period. In the present experiment several measurements of growth were made to determine how net production varied throughout the winter. We have shown that the mean growth rates of all strains in the January–February periods for two years (see Fig. 1) were significantly greater than those in the December–January periods, and therefore minimum growth corresponded with the shortest photoperiods. As irradiance and photoperiod increased, growth rate increased in January–February and almost doubled from January–February to February–March even though the mean seawater temperature remained low or actually declined as in 1979–80. Our data provide support for the speculation (Bird et al. 1979) that low temperature alone should not cause a cessation of growth in *C. crispus*.

Chondrus crispus commonly inhabits the lower littoral and sublittoral zones to depths of 10–19 m where solid substratum exists (Mathieson and Prince 1973). The geographical distribution from subarctic to warm temperate regions of the North Atlantic implies that the alga is tolerant of a wide range of temperatures. Although it seems generally agreed that the growth of *C. crispus* in nature is minimal between November and March (Marshall et al. 1949; Mathieson and Prince 1973), few direct measurements have been reported. Taylor (1971)

TABLE 3. Net production and subsequent growth rates of *C. crispus* isolates overwintered in uncovered, outdoor tanks during 1982–83 and 1983–84.

	Isolate	Stocking density ($kg \cdot m^{-2}$)	Winter[a] Net production ($kg \cdot m^{-2}$) $\bar{X}$	SD	*n*	Spring[b] Net production ($kg \cdot m^{-2}$) $\bar{X}$	SD	*n*	Growth rate ($kg \cdot m^{-2} \cdot wk^{-1}$) $\bar{X}$	SD	*n*
1982–83	T4	5	−0.33	—	2	−0.22	—	2	0.25	—	2
	T4	10	−1.79	—	2	—	—	—[c]	—	—	—
	BH–H	5	0.14	±0.06	4	0.09	±0.08	3[d]	0.42	±0.04	3
	BH–H	10	−1.53	±1.13	4	−0.31	—	1[c]	0.31	—	1
1983–84	BH–H	5	0.57	±0.05	3	−0.07	±0.18	3	0.45	±0.09	3
	BH–H	7.5	0.60	±0.13	3	0.10	—	2[d]	0.40	—	2
	BH–H	10	0.47	±0.04	3	−0.43	±0.16	3	0.34	±0.07	3
	BH–D	5	0.99	—	2	−0.01	—	2	0.53[e]	—	2

[a]Experiments were initiated on Dec. 8 in 1982 and on Dec. 6 in 1983. Agitation and seawater supplies were discontinued on Dec. 13 in 1982 and Dec. 19 in 1983 and resumed Mar. 15 and 16 in 1983 and 1984, respectively.

[b]The spring period included a recovery phase during which net production was recorded and a subsequent growth phase. The former was Mar. 16 – Apr. 6 in 1983 and Mar. 16 – Apr. 4 in 1984; the latter was Apr. 6–22 in 1983 and Apr. 4–30 in 1984.

[c]Number of replicates reduced because of mortality.

[d]Number of replicates reduced because algae were used in other experiments.

[e]Growth period was Apr. 3–24, 1984.

observed growth of *C. crispus* on Prince Edward Island and at Point Lepreau, N.B., and near St. Andrews, Scotland. He concluded that "growth seems to be virtually stopped in winter even in areas of above freezing temperature." Chen and Taylor (1980) also found no change in the mean width of *C. crispus* plants at Cape d'Or, N.S., between November and March. Similar growth patterns were recorded from New Hampshire (Mathieson and Burns 1975) and Massachusetts (Prince and Kingsbury 1973).

Field observations, however, do not distinguish amongst the environmental variables that may limit growth. The most important of these are irradiance, photoperiod, nutrients, and temperature. Several laboratory studies on the growth of *C. crispus* have been reported, but little attention was directed towards growth under winter conditions. Ring (1970) found that *C. crispus* spores collected in Maine would germinate and develop at 5°C in culture. At high and medium irradiances (500 ft-c ≈ 0.7 $MJ \cdot m^{-2} \cdot d^{-1}$ and 130 ft-c ≈ 0.18 $MJ \cdot m^{-2} \cdot d^{-1}$, respectively), discs, rhizoids, and upright stalks of *C. crispus* were capable of approximately doubling their linear dimensions (diameter and/or length) in 14–20 d on an 8:$\overline{16}$ h photoperiod. At low irradiance (16 ft-c ≈ 0.02 $MJ \cdot m^{-2} \cdot d^{-1}$) the dimensions doubled in 22–32 d at 5°C and the same photoperiod. A doubling time of 25 d was reported by Bird et al. (1979) for young *C. crispus* gametophytes (originating from Pomquet Harbour, N.S., plants) grown at 5°C under a long photoperiod (16:$\overline{8}$ h) at moderately high levels of photosynthetically active irradiance (145 $\mu E \cdot m^{-2} \cdot s^{-1}$ ≈ 1.8 $MJ \cdot m^{-2} \cdot d^{-1}$, PAR). A different strain of *C. crispus* (from Cape d'Or, N.S.), however, showed very little growth after 5 mo in culture at 5°C under a 16:$\overline{8}$ h photoperiod and an irradiance of 60 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Chen and Taylor 1980). Similarly, germling tetrasporophytes of *C. crispus* cultured from New Hampshire material exhibited little growth at 3°C with a 12:$\overline{12}$ h photoperiod and a total irradiance of 440 ft-c (≈0.9 $MJ \cdot m^{-2} \cdot d^{-1}$) (Burns and Mathieson 1972). Enright and Craigie (1981) showed that temperature-acclimated *C. crispus* strain T4 which grew at approximately 15% per week at 2°C would increase its growth rate 2.3-fold when grown at 5°C under otherwise parallel conditions (16:$\overline{8}$ h photoperiod providing 2.5–2.6 $MJ \cdot m^{-2} \cdot d^{-1}$, PAR). Somewhat lower growth rates (11–13% per week; doubling time of 40–45 d) can be calculated from the data of Simpson and Shacklock (1979) for the same *C. crispus* strain cultured at 3°C. In the latter case the natural irradiance in the greenhouse during August and September was approximately 4.2 $MJ \cdot m^{-2} \cdot d^{-1}$ (PAR) with a photoperiod of 14:$\overline{10}$ h.

None of the above laboratory experiments can be related directly to outdoor conditions because they did not adequately reflect the irradiance and photoperiods in winter. Braud and Delépine (1981) presented data for *C. crispus* stocked at 2.1 $kg \cdot m^{-2}$ in outdoor tanks in northern France (≈50°N) showing that net growth (fresh weight) was approximately 0.12, 0.04, 0.04, 0.10, 0.12, and 0.20 $kg \cdot m^{-2} \cdot wk^{-1}$ for the months of November to April, respectively. The corresponding mean irradiances (PAR) and temperatures in their experiment were 1.5, 1.3, 1.5, 2.2, 3.7, and 4.4 $MJ \cdot m^{-2} \cdot d^{-1}$ and 13.0, 9.2, 5.4, 9.1, 10.3, and 13.9°C, respectively. Whereas our data (Fig. 1) confirm that growth is minimal during the December–January period, our growth rates are two to four times higher throughout the winter. This cannot be attributed to differences in irradiance or photoperiod, and it is unlikely that the small discrepancy in stocking densities is an important variable between the experiments. The use of different strains of *C. crispus* may account for some of the variation; however, the mean water temperatures were considerably higher in France than in Nova Scotia. In the former case, the combination of higher temperatures with the low winter irra-

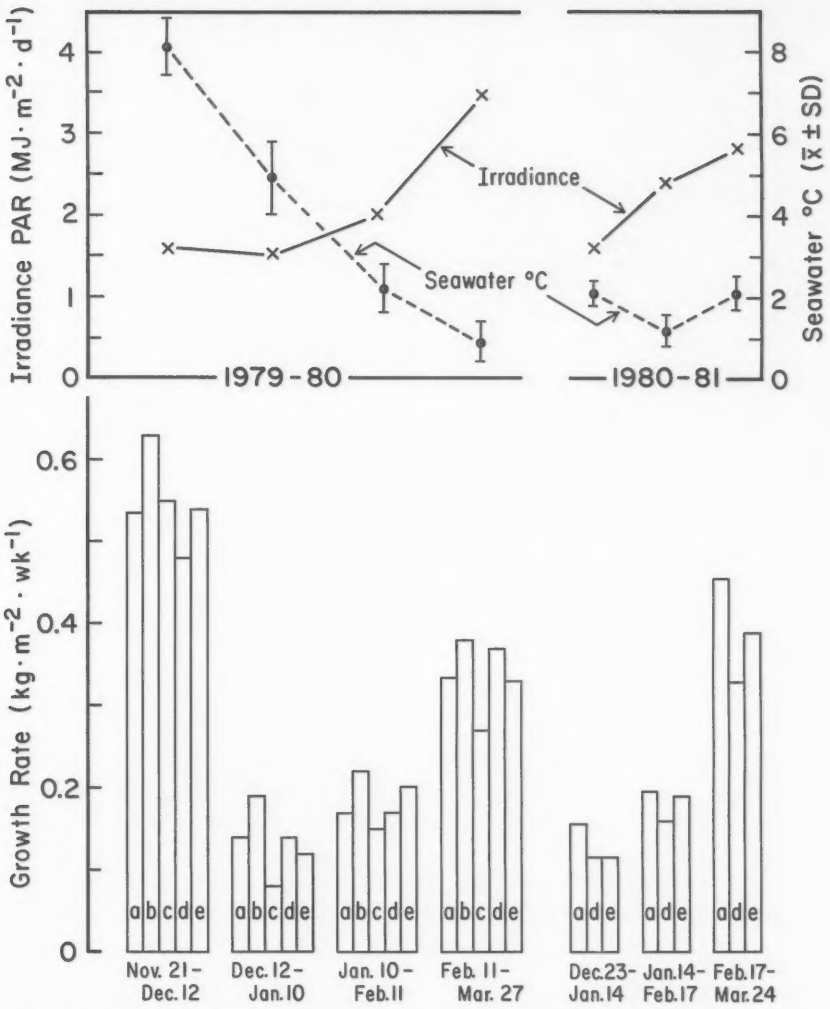


FIG. 1. Growth of *C. crispus* isolates during the winters of 1979–80 and 1980–81 in tanks in an unheated, polyethylene-covered structure. Air agitation and seawater were provided continuously. (a) Isolate T4, average of duplicate cultures; (b) isolate T4G, single culture; (c) isolate T4dG, single culture; (d) isolate ARL-16, single culture in 1979–80 and average of duplicate cultures in 1980–81; (e) isolate 750128 C, single culture in 1979–80 and average of duplicate cultures in 1980–81.

diance and short photoperiod would probably divert more fixed carbon to respiration and result in a low net production and growth rate.

Seasonal characteristics for irradiance, photoperiod, and temperature measured in outdoor tanks near Halifax, N.S., were established in growth chambers in which small plants of *C. crispus* strain T4 were cultured (Bidwell et al. 1984). Growth measured through the simulated winter gave calculated net productions (fresh weight basis) of approximately 0.29, 0.15, 0.31, 0.22, and 0.84 $kg \cdot m^{-2} \cdot wk^{-1}$ for the months of November through March, respectively. The production calculated for December and February is in reasonable accord with our data (Fig. 1). The lack of close correspondence between our data sets for November, January, and March does not seem to be related to temperature, but may reflect idiosyncracies of outdoor culture systems not reproduced in the growth chambers.

In undisturbed outdoor culture tanks we have frequently measured a surface layer of ice of 35 cm depth and found numerous large crystals of ice in the free brine layer amongst the *C. crispus* fronds. We have recorded salinities up to 60‰ in samples withdrawn from the brine layer. From the available data we suggest that *C. crispus* grows poorly, if at all, at salinities of ≥50‰ although reasonable growth can be achieved for up to 3 wk at 38–40‰ (Burns and Mathieson 1972; Neish et al. 1977; Bird et al. 1979). At low temperatures, however, the salinity is increased by a freezing out process and ice may be formed within the algal frond. Kanwisher (1957) found that at −15°C, 74% of the water in the *C. crispus* thallus was present as ice. He further determined that the respi-

ration of *C. crispus* between −10 and 0°C had a Q_{10} of 15. The extremely low respiration rates coupled with the tolerance of *C. crispus* to very high salinities appear to be the main factors permitting the survival of this alga in the aboveground tanks of seawater at ambient air temperatures that may reach −15 to −20°C. Since the addition of O_2 appeared to be beneficial at high stocking densities, we suggest that anaerobiosis resulting from plant respiration may be a cause of mortality in the undisturbed tanks. The resumption of rapid growth in April demonstrated that *C. crispus* sustained no permanent damage. As the aboveground tanks were subjected to more severe environmental conditions than would occur in similar below ground tanks or ponds, no difficulty is anticipated in maintaining a viable inoculum of *C. crispus* on a large scale.

Our experiments have shown that positive net production of *C. crispus* occurs during each winter month in running seawater in tank cultures. Similarly, winter growth of natural stands may be expected in our area providing that the coastal zone is not ice covered. We further conclude that both haploid and diploid strains of *C. crispus* can be overwintered in a healthy, viable state in shallow (approximately 1 m deep) tanks. No agitation or fresh seawater need be supplied during the period of ice cover. Stocking densities should not exceed 10 $kg \cdot m^{-2}$ on a fresh weight basis. These simple, inexpensive procedures are directly applicable to commercial cultivation of Irish moss where it is necessary to overwinter a large vegetative inoculum.

Acknowledgments

We thank Messrs. D. R. Robson for helpful engineering advice and L. Staples for expert technical assistance.

References

BIDWELL, R. G. S., N. D. H. LLOYD, AND J. MCLACHLAN. 1984. The performance of *Chondrus crispus* (Irish moss) in laboratory simulations of environments in different locations. Proc. Int. Seaweed Symp. 11: 292–294.

BIRD, N. L., L. C.-M. CHEN, AND J. MCLACHLAN. 1979. Effects of temperature, light and salinity on growth in culture of *Chondrus crispus*, *Furcellaria lumbricalis*, *Gracilaria tikvahiae* (Gigartinales, Rhodophyta), and *Fucus serratus* (Fucales, Phaeophyta). Bot. Mar. 22: 521–527.

BRAUD, J. P., AND R. DELÉPINE. 1981. Growth response of *Chondrus crispus* (Rhodophyta, Gigartinales) to light and temperature in laboratory and outdoor tanks culture. Proc. Int. Seaweed Symp. 10: 553–558.

BURNS, R. L., AND A. C. MATHIESON. 1972. Ecological studies of economic red algae. II. Culture studies of *Chondrus crispus* Stackhouse and *Gigartina stellata* (Stackhouse) Batters. J. Exp. Mar. Biol. Ecol. 8: 1–6.

CHEN, L. C.-M., K. MORGAN, AND F. J. SIMPSON. 1982. Selection of tetrasporophytes of Irish moss. Bot. Mar. 25: 35–36.

CHEN, L. C.-M., AND A. R. A. TAYLOR. 1980. Investigations of distinct strains of *Chondrus crispus* Stackh. I. Field and laboratory observations. Bot. Mar. 23: 435–440.

ENRIGHT, C. T., AND J. S. CRAIGIE. 1981. Effects of temperature and irradiance on growth and respiration of *Chondrus crispus* Stackh. Proc. Int. Seaweed Symp. 10: 271–276.

GUIRY, M. D. 1981. *Chondrus cripsus* Stackhouse 'T4' is a male clone (Rhodophyta). Phycologia 20: 438–439.

KANWISHER, J. 1957. Freezing and drying in intertidal algae. Biol. Bull. Woods Hole 113: 275–285.

MARSHALL, S. M., L. NEWTON, AND A. P. ORR. 1949. A study of certain British seaweeds and their utilization in the preparation of agar. L. Newton [ed.] His Majesty's Stationery Office, London. 184 p.

MATHIESON, A. C., AND R. L. BURNS. 1975. Ecological studies of economic red algae. V. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. J. Exp. Mar. Biol. Ecol. 17: 137–156.

MATHIESON, A. C., AND J. S. PRINCE. 1973. Ecology of *Chondrus crispus* Stackhouse. Proc. Nova Scotian Inst. Sci. 27 suppl.: 53–79.

NEISH, A. C., AND C. H. FOX. 1971. Greenhouse experiments on the vegetative propagation of *Chondrus crispus* (Irish moss). Tech. Rep. No. 12, Atlantic Regional Laboratory, National Research Council of Canada, Halifax, N.S. 35 p.

NEISH, A. C., P. F. SHACKLOCK, C. H. FOX, AND F. J. SIMPSON. 1977. The cultivation of *Chondrus crispus*. Factors affecting growth under greenhouse conditions. Can. J. Bot. 55: 2263–2271.

PRINCE, J. S., AND J. M. KINGSBURY. 1973. The ecology of *Chondrus crispus* at Plymouth, Massachusetts. II. Field studies. Am. J. Bot. 60: 964–975.

RING, P. D. 1970. Developmental and ecophysiological studies of *Chondrus crispus* (L.) Stackh. M.Sc. thesis, University of Maine, Orono, ME. 73 p.

SHACKLOCK, P. F., AND G. B. CROFT. 1981. Effect of grazers on *Chondrus crispus* in culture. Aquaculture 22: 331–342.

SHACKLOCK, P. F., D. R. ROBSON, AND F. J. SIMPSON. 1975. Vegetative propagation of *Chondrus crispus* (Irish moss) in tanks. Tech. Rep. No. 21, Atlantic Regional Laboratory, National Research Council of Canada, Halifax, N.S. 27 p.

SIMPSON, F. J., A. C. NEISH, P. F. SHACKLOCK, AND D. R. ROBSON. 1978. The cultivation of *Chondrus crispus*. Effect of pH on growth and production of carrageenan. Bot. Mar. 21: 229–235.

SIMPSON, F. J., AND P. F. SHACKLOCK. 1979. The cultivation of *Chondrus crispus*. Effect of temperature on growth and carrageenan production. Bot. Mar. 22: 295–298.

TAYLOR, A. R. A. 1971. Growth studies of *Chondrus crispus* in Prince Edward Island, p. 29–36. Proc. Meet. Can. Atl. Seaweeds Ind., Charlottetown, P.E.I., October 5–6, 1971. Secretariat, Industrial Development Branch, Fisheries Service, Ottawa, Ont.

Environmental and Parental Influences on Age at Maturity in Sockeye Salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia

Randall M. Peterman,[1] Michael J. Bradford,[1] and Judith L. Anderson

Natural Resource Management Program, Simon Fraser University, Burnaby, B.C. V5A 1S6

Peterman, R. M., M. J. Bradford, and J. L. Anderson. 1986. Environmental and parental influences on age at maturity in sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 43: 269–274.

Commercial fisheries possess the potential for applying strong selection on size or age at maturity in the populations they exploit. It is therefore important to know the extent to which these traits are inherited. We examined regressions of the mean age at maturity of cohorts of offspring on the mean ages of the female and male spawners which produced them for four populations of sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia. Unlike previous researchers, we found that neither genetic nor maternal effects are important, relative to environmental variables, in influencing year-to-year variation in age at maturity in these stocks. The differences between our findings and earlier ones are due to a longer data series and more complete population statistics than were available previously. We further analyzed the age structure of the Adams River population, which has a cyclic pattern of abundance. Fluctuating population density appeared to account for variation in age structure among cycle years in the Adams stock. We concluded that serious concerns about the long-term effects of size-selective fishing on mean age at maturity are probably not warranted for Fraser River sockeye.

Les pêches commerciales ont la capacité d'exercer une grande sélection sur la taille ou l'âge atteint à la maturité des poissons de populations exploitées. Il est donc important de savoir jusqu'à quel point ces caractères sont transmis d'une génération à l'autre. Nous avons examiné les régressions de l'âge moyen à la maturité de cohortes de descendants par rapport à l'âge moyen des reproducteurs mâles et femelles qui les ont produits pour quatre populations de saumon rouge (*Oncorhynchus nerka*) provenant du fleuve Fraser en Colombie-Britannique. Contrairement aux chercheurs précédents, nous avons trouvé que ni les facteurs génétiques ni les facteurs maternels ne sont importants, si on les compare aux variables du milieu, pour influencer les variations d'une année à l'autre de l'âge à la maturité de ces stocks. Les différences observées entre nos résultats et les résultats précédents sont attribuables à une série de données plus longue et à des statistiques plus complètes qu'auparavant sur les populations. Nous avons analysé plus en détail la structure par âge de la population de la rivière Adams, dont l'abondance varie de façon cyclique. Les fluctuations de la densité de la population semblaient expliquer les variations de la structure par âge observées entre les années du cycle dans le stock de la rivière Adams. Nous avons conclu que les sérieuses inquiétudes concernant les effets à long terme de la pêche en fonction de la taille sur l'âge moyen à la maturité ne sont probablement pas justifiées en ce qui concerne le saumon rouge du fleuve Fraser.

Received May 13, 1985
Accepted October 16, 1985
(J8238)

Reçu le 13 mai 1985
Accepté le 16 octobre 1985

Fisheries biologists have long been concerned that fish stocks may change genetically in response to selection pressures exerted by the fishery (e.g. Ricker 1981). It would be advantageous, then, if the potential for undesirable genetic changes in important traits could be quantified for each stock, so that appropriate management measures could be employed to prevent such changes.

Age at maturity in salmon is an example of a trait in which genetic change could be important for fisheries. Age at maturity and size are highly correlated in sockeye salmon (*Oncorhynchus nerka*) (e.g. Bilton 1971), and size affects fecundity and economic value of the catch. Because of the close relation between size and age, age at maturity comes under selection when fishermen employ size-selective gear. To assess the potential for change in age at maturity, three components of the problem must be examined: (1) the direction and magnitude of selection, (2) the relative importance of parental age versus environmental influences on offspring age, and (3) the response to selection.

The intensity and scope of selection have been studied in several sockeye stocks (Peterson 1954; Killick and Clemens 1963; Todd and Larkin 1971; Ricker 1982; Rogers and Poe 1984) with the consensus being that there is potential for strong directional selection on size and age, though current fishing practices sometimes do not maintain a consistent directional selection over a long period. Because of this potential, it is important to know whether individual stocks of sockeye salmon will respond with genetic changes in age at maturity, if strong directional selection pressures should be imposed by fishermen.

[1] Current address: Southwest Fisheries Center, National Marine Fisheries Service, 8604 La Jolla Shores Drive, La Jolla, CA 92038, USA.

The relative importance of genetic and environmental effects on age at maturity of sockeye salmon is not yet apparent. Both parental (Godfrey 1958; Ricker 1972) and environmental (Peterman 1985) influences exist in determining age at maturity of sockeye, as in other salmonids (Gardner 1976; Naevdal 1983; Ricker 1981; Saunders et al. 1983; Sutterlin and MacLean 1984; Thorpe et al. 1983). As in other species, it is undoubtedly true that the range of potential age at maturity for sockeye (3−8+ yr) is set within a stock by some genetically determined physiological constraints. However, it is not clear whether genetic factors are important in determining *interannual variation* in age at maturity within exploited sockeye populations. We focused on this between-year variation in the age at maturity of different brood classes of sockeye.

The third component, the response to selection, has been examined directly by several authors who have looked for historical trends in size in sockeye salmon, with the assumption that a change in size over time could be a genetic response to size-selective fishing. Killick and Clemens (1963) observed no change in size of Fraser River sockeye salmon over the years 1915−60. Ricker (1981, 1982) observed a weak tendency toward smaller size at harvest in several British Columbia stocks and concluded that any response to size-selective fishing in this species must be complicated by the presence of several returning age classes and by environmental changes.

In this paper, we focus on the second component of the problem and attempt to assess the relative importance of parental and environmental contributions to interannual variation in age at maturity in several stocks of sockeye salmon from the Fraser River, British Columbia. These stocks were chosen because of the completeness of their data. Unlike most age data used by previous researchers on British Columbia sockeye (Godfrey 1958; Killick and Clemens 1963; Larkin 1971; Ward and Larkin 1964; Ricker 1972), the data that we analyzed included estimates of age structure and abundance in both catch and escapement, enabling us to characterize separately the mean ages of parents and of the complete population of their offspring. In addition, one of the four stocks we examined, Adams River, is unique because of the wide variation in paternal age.

Methods

Data Sources

In the Gilbert−Rich notation, salmon ages have two components: the total age of the fish and the age at which it entered the ocean (indicated as a subscript). Thus, a fish of age 4_2 is in its fourth year of life since hatching, and it entered the ocean during its second year, after living one winter as a fry in fresh water. Similarly "sub-3" fish are those that smolted after spending two winters in freshwater. In this paper, the "total age" of fish is the year of life in which they mature.

Data on four Fraser River watershed sockeye stocks (Adams River, Chilko Lake, Cultus Lake, and Stellako River) were provided by the International Pacific Salmon Fisheries Commission (IPSFC) (J. Roos and J. Woodey, New Westminster, B.C., pers. comm.). Data for brood years 1950−76 were broken down by age and smolt type of catch and escapement but sex-specific data were available only for escapements. The age groups 3_2, 4_2, and 5_2 comprise 98% of the total returns.

The Adams River sockeye population is notable for its marked 4-yr cycle of abundance, and hence it constitutes a useful "natural experiment" for testing hypotheses about age at maturity (Ricker 1972). Because more than 90% of these fish return at age 4, the 4 yr of the cycle can be considered to be roughly separate populations or lines, with the dominant (most abundant) cycle year designated Line 1, following the convention of Ward and Larkin (1964) and Ricker (1972). Line 1 refers to populations that spawned in 1970, 1974, 1978, etc., Line 2 refers to brood years 1971, 1975, 1979, etc., and so on for Lines 3 and 4. Mean abundances by line are given at the bottom of Table 2.

Analysis

Within each stock, the offspring from a given brood year were represented by the total returns (catch plus escapement) of fish from that brood class, summed over all the years in which they returned as mature adults. Parents for a given brood year were represented by the total escapement for that year. Each year-class of offspring or parents was further broken down by sex or smolt type, where data permitted, and the mean age of maturity was calculated as the weighted average age for that subgroup. We examined four related age measures: total age, total age of sub-2 fish, smolt age, and ocean age (total age minus smolt age).

We fit linear time trends by ordinary regression for each group of offspring and spawners and each measure of age of maturity because significant time trends could affect the interpretation of our results. Of the 16 time trend regressions for returns of the Fraser River stocks (4 age measures × 4 stocks, sexes combined), only one (Chilko, total age) was significant at the 0.05 level ($r = -0.4$, $P = 0.04$, $n = 28$). Only 11 of the 16 regression coefficients were negative, which is not a significant deviation from the expected equal frequency of + and − signs ($P = 0.21$ by a signs test). Therefore, we used raw data rather than time trend residuals for our analysis.

The data for total returns (offspring) were not available by sex, whereas spawning populations were. Therefore, we calculated separate regressions of offspring mean age (sexes pooled) upon mean age of male parents and of female parents for the four age measures (total age, smolt age, ocean age, and sub-2 total age) in each of three stocks (Adams, Chilko, and Cultus). The fourth stock, Stellako, displayed virtually no variance in smolt age. Because of this, the other three age measures were not independent, so we only analyzed ocean age for this stock. Thus, a total of 13 offspring-on-parent regressions were calculated for each sex of spawner.

Results and Discussion

Offspring-on-Parent Regressions

Our results produced no evidence that parental effects are important in comparison with environmental determinants of variation in age at maturity. Of the offspring-on-parent regressions calculated for each sex (Table 1), only one was significant, Adams total age (Fig. 1A and 1B). This case is discussed in detail later. We expected ocean age to be the most likely age measure to show significant offspring-on-parent regressions because of its high correlation with body size (e.g. Rogers 1980), because of the relation between size and reproductive success in salmon (van den Berghe and Gross 1984), and because ocean age alone produced significant offsprint-on-parent regressions in Alaskan stocks (Peterman 1985). However, there is no significant offspring-on-parent

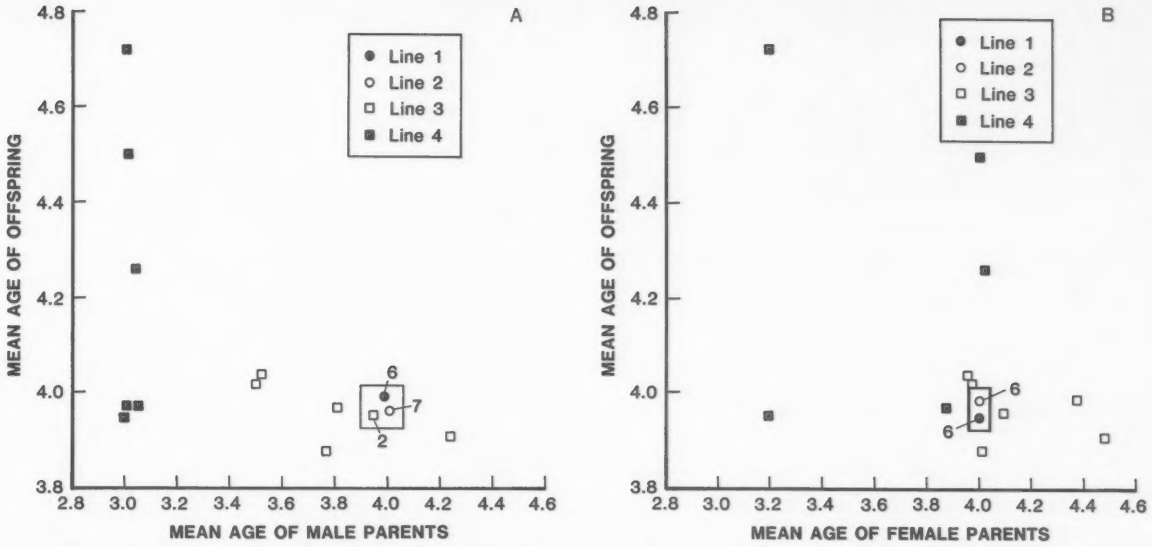


FIG. 1. Regression of mean values of the total age at maturity of offspring (sexes pooled) on mean total age for (A) male and (B) female sockeye salmon spawners of the Adams River. Males: $Y = 4.99 - 0.26X$, $P = 0.001$; females: $Y = 5.39 - 0.34X$, $P = 0.012$. Data cover brood years 1950–76. "Lines" are defined in the text.

TABLE 1. Regressions of mean age of offspring (sexes pooled) on mean age of spawners (sexes separated) for four Fraser River sockeye stocks and four age measures (b = regression slope; P = probability for $b = 0$; N = sample size in years; *represents a significant case).

		Offspring age on male spawner age			Offspring age on female spawner age		
	Stock	b	P	N	b	P	N
Ocean age	Adams	0.02	0.31	27	0.06	0.07	27
	Chilko	0.11	0.11	25	0.09	0.29	28
	Cultus	−0.22	0.13	27	−0.41	0.33	27
	Stellako	0.07	0.47	27	0.13	0.20	27
Total age	Adams	−0.26	0.001*	27	−0.34	0.01*	27
	Chilko	0.14	0.18	25	0.12	0.18	28
	Cultus	−0.19	0.18	27	−0.43	0.23	27
Smolt age	Adams	−2.09	0.44	27	−1.02	0.19	27
	Chilko	0.18	0.11	25	0.12	0.21	28
	Cultus	−0.04	0.87	27	0.12	0.40	27
Sub-2 total age	Adams	−0.004	0.80	28	−0.03	0.28	28
	Chilko	0.07	0.22	29	0.09	0.26	29
	Cultus	0.06	0.51	28	−0.30	0.49	28

regression for this age measure, nor is there a strong tendency toward positive slopes for any age measure (Table 1), as predicted by an additive genetic model. Therefore, on the basis of current data, we do not expect that Fraser River sockeye will respond to size-selective fishing with changes in age at maturity.

Adams River Case

The only exception to the pattern of nonsignificant offspring-on-parent regressions was Adams River total age. While one significant result might be expected by chance alone given the number of regressions performed, closer examination of this case reveals an interesting effect of abundance. In the Adams River stock, a significant inverse relationship between offspring and parents appears in both sexes of spawners (Fig. 1A and 1B).

Bilton (1970, 1971) proposed a mechanism which predicts an inverse relationship between age at maturity of offspring and that of the female parent for populations of sockeye salmon with little variance in smolt age. He showed that large (relatively old) female sockeye salmon tend to produce larger eggs than their younger conspecifics. These eggs in turn hatch into large fry, and if these fry maintain their size superiority throughout their lives, they will tend to mature earlier (and smaller) than those which grow more slowly. The significant Adams River regressions might be interpreted to be consistent with Bilton's

TABLE 2. Percent of total returns (catch and escapement) in each age category for Adams River sockeye salmon according to line year of brood as defined in the text. In these 4-yr cycles of abundance, the dominant or most abundant year is labeled Line 1. Mean abundances of each line are given at bottom of the table. Mean ages of parents of these offspring are shown on *X*-axes in Fig. 1A and 1B. Data are averaged over brood years 1950–76 and cover six or seven generations of fish.

	Line year of brood			
Age	1	2	3	4
3_2	3.8	1.9	7.0	4.8
4_2	95.3	97.9	89.4	70.5
5_2	0.22	0.15	1.83	0.0
4_3	0.02	0.0	0.0	2.5
5_3	0.65	0.03	1.81	22.2
Average abundance (thousands)	6584	1379	18	34

maternal effects hypothesis because the high correlation between the sexes of spawners in their age at maturity ($r = 0.60$, $P < 0.001$) would tend to make the slope negative for the regression on male parents, too. However, evidence in Fig. 1B argues against the operation of Bilton's maternal effects in this stock. Two Line 4 years had unusually low maternal mean age, but only one produced offspring which returned later than average. Two other Line 4 years produced offspring of relatively high mean age at return, but the mean age of the female spawners for these years falls in the center of the historical distribution of ages.

Inspection of Figures 1A and 1B and Table 2 reveals that the pattern of offspring ages is instead indirectly attributable to the strong 4-yr cycle of abundance in the Adams River stock, rather than to any parental influence. This conclusion is reached by the following observations.

There is wide variation in age at maturity of Adams River sockeye spawners, especially males (*X*-axis of Fig. 1A). This is because each year, a small proportion of fish return as jacks (age 3_2 fish, mostly males). The dominant line (Line 1) of the cycle produces so many more fish than the other cycle years (see bottom line of Table 2) that its jacks, returning at age 3 along with age 4 fish of Line 4, greatly outnumber the age 4 fish spawning in that year. Thus, in these Line 4 years (just prior to the dominant years) there is an unusually low paternal (and sometimes maternal) mean age (solid squares in Fig. 1A and 1B).

The predominance of jacks in Line 4 spawning populations did not result in a higher proportion of jacks in the offspring of this Line (Table 2), as would be predicted by the genetic model. Instead, in years when jacks are abundant among male spawners, a wide variety of mean total ages results, including the highest mean ages observed for any line (Fig. 1A).

The high values of mean total age for offspring produced by Line 4 years (in which jacks predominate among their parents) result from an unusually high frequency of fish which smolted as sub-3s, instead of sub-2s. Line 4 is the only cycle year which produces significant proportions of 4_3 and 5_3 offspring (Table 2).

The high proportion of sub-3 fish among Line 4 offspring may be caused by a predation buffering effect (Neave 1953; Ward and Larkin 1964). Line 4 offspring which smolt as sub-3s will migrate to sea with the much more abundant cohort of sub-2 smolts from the dominant Line 1. Because predators become satiated at high prey abundances, these Line 4 sub-3s may experience a lower percentage loss to predation than their cohorts which smolted at age 2 along with a much less abundant smolt population. This buffering effect would lead to the larger than average portion of sub-3s seen in Table 2 for Line 4 offspring.

An alternative hypothesis, competition in freshwater, is not a plausible explanation for the predominance of the sub-3s among Line 4 offspring. Unlike most sockeye stocks, Adams River fish do not show a larger proportion of sub-3 smolts in high abundance years, even though these cohorts have relatively slow freshwater growth (Killick and Clemens 1963). Furthermore, the very abundant Line 1 offspring migrate to the rearing lake 1 yr *after* Line 4 fry, and therefore do not deplete zooplankton in a way which would affect Line 4 offspring (Ward and Larkin 1964; IPSFC 1978). If anything, the depletion of zooplankton by the abundant Line 1 smolts should create more sub-3s among Lines 2 and 3, which does not occur (Table 2).

Thus the inverse relationships between total age of offspring and total age of spawners for the Adams River cannot be interpreted as support for Bilton's or the genetic hypotheses. It is much more plausibly interpreted as evidence that population density and predation are important environmental determinants of the mean age at maturity of cohorts within this stock.

Comparison with Earlier Research

Our strongest test of the parental effect hypothesis, on the Adams River sockeye stock, failed to show any significant effect of parental age on offspring age. This contrasts with the conclusions reached on that same stock by Ward and Larkin (1964) and Ricker (1972, although he admits the evidence is weak). This difference in conclusions arises because the age composition data which we used to derive Table 2 differ from those of Ward and Larkin (1964, p. 100) and Ricker (1972, p. 88). Their tables report much higher proportions of jacks among the progeny than do our data. However, their tables are based on escapement (spawner) data only, and thus fail to take into account the significant selective removal of older fish by the fishery (Peterson 1954; Killick and Clemens 1963). In addition, Ward and Larkin (1964) included data from only six brood years and Line 4 is represented by only one year. In contrast, our age structure data include both catch and escapement samples, and cover 27 brood years (six or seven generations for each line). Killick and Clemens (1963) used age structure data sampled before the onset of any size-selective fishing, but their data were from all Fraser River sockeye stocks combined, not broken down by stock as in our case.

Also in contrast with our results, Godfrey (1958) examined two British Columbia sockeye populations (Skeena River and Rivers Inlet) *using catch data only*, and concluded that genetic factors influenced age at maturity. He found strong positive correlations between abundance of age 4_2 fish in the catch in a given year and abundance of 4_2 catches 4 yr later; age 5_2 fish produced a similar positive correlation at an interval of 5 yr. However, there was no correlation between numbers of 5_2 fish in the catch and 4_2 fish 4 yr later, or between 4_2 catches and 5_2 fish 5 yr later, though such a correlation is predicted by Bilton's hypothesis. Not only does Godfrey's analysis suffer from dealing with catch data only, it also relies heavily on the assumption that environmental fluctuations occur at random,

rather than periodically. This assumption may be true in some cases, but in the Adams River population, the cyclic pattern in abundance does not appear to be genetically determined, and such environmental factors as depensatory predation probably change cyclically along with population density, thus enhancing or possibly causing the cycle (Ward and Larkin 1964; Larkin 1971).

The absence of parental effects documented in this paper provides one possible explanation of the lack of any significant long-term time trend in size (Ricker 1981; Killick and Clemens 1963). Another explanation is that size-selective fishing has not been consistently unidirectional because of the between-year variation in fish size and the failure of mesh sizes of gill nets to change accordingly (Killick and Clemens 1963). Finally, a trend in ocean temperature and its effect on ocean growth may be masking a change in mean size and age at maturity which would otherwise occur (Ricker 1981, 1982). However, we suggest that even if fishing selection were to become consistently directional and even if ocean temperature were to stabilize, there would be little response in age at maturity of Fraser River sockeye.

Qualifiers

Errors associated with the abundance estimation of the less numerous lines of Adams River sockeye would not affect our conclusions. The average harvest rate of age 3_2 fish from Line 4 was 58%, similar to the 51% estimated for the more abundant age 3_2 fish from Line 1. For the proportion of age 3_2 fish in Line 4 (Table 2) to double to 9.6%, for example, the catch of 3_2 fish would have to have been 2.7 times the currently estimated catch. This is unlikely, given the similarity of harvest rates of 3_2 fish for lines of greatly differing abundance, and our conclusion is probably valid that the jack-dominated Line 4 spawners did not produce more jacks than in other years.

The high proportion of 5_3 fish observed in the Line 4 returns could be subject to considerable sampling error, since they return with the abundant Line 1 4_2 fish. However, if the true proportion of age 5_3 fish in Line 4 was in actuality similar to the other lines (1%), then the abundance of 5_3 fish would have to have been overestimated by a factor of 28 to obtain the results of Table 2.

We concluded that there is no genetic influence on the occurrence of early maturation of Adams River sockeye. However, this conclusion is dependent on the assumption that the jacks mate successfully in approximate proportion to their abundance. In the Line 4 years when jacks are common in the spawning population (Fig. 1), the "sneaking" behavior described by Gross (1985) should enable jacks to contribute a higher percentage of the sperm to fertilize eggs than when jacks are less common. Because jacks do not predominate among the offspring of these brood years in Adams River, fluctuating population density of offspring instead appears to be an important environmental influence on their age at maturity.

General Discussion

We must emphasize that our parent–offspring regression analysis has not measured the formal heritability (h^2) of age at maturity. On this point our results are not comparable with studies like those of Gjerde (1984), Refstie and Steine (1978), Refstie (1980), and Herschberger et al. (1982), who have estimated h^2 of age at maturity using controlled breeding schemes in the regulated environment of hatcheries or laboratories. If an estimate of heritability is to be based on correlations among relatives, it must include data from many identified families breeding at the same time, rather than means of cohorts from different years, as in our analysis. If we could have identified individual breeding pairs and their offspring, we would have been more likely to detect positive relationships, especially since sockeye salmon do tend to mate assortatively (Hanson and Smith 1967). In addition, our estimates probably underestimate the slope of the true relationship between the age of maturity of cohorts of offspring and their parental populations, because we have not identified the actual spawning individuals within the escapement. Nonbreeding fish increase the error of mean age estimates for parental populations. This error in measurement of the X variate causes the absolute value of the estimated slope of the regression to be lower than the absolute value of the true slope (Ricker 1973).

Even though it may be easier to measure positive relationships with advantageous breeding designs in controlled environments, our results from wild populations are more relevant for management of stocks for which most of the spawning occurs in natural environments. Unlike a breeding program for domesticated animals, management of wild fish populations takes place on a gross population level with measurement error and environmental variation present. Concern about size-selective fishing and potential for genetic change in the population is important only if directional selection pressure can overcome environmental variation to cause a detectable response.

Our analysis, based as it is on time series data, cannot conclusively reject hypotheses, but rather should serve to suggest potential experiments. In addition to historical analysis, then, it is important for managers to view their fisheries not just as economic systems, but also as experimental ones. For example, breeding experiments carried out in spawning channels could help to clarify the relative contribution of maternal and genetic effects on age at maturity of sockeye salmon, as they have in other species. Alternatively, strong directional selection could purposely be applied to a population for a specified period to assess its response to selection and its capacity to recover when the selection pressure is removed. Such experiments would provide at least some of the information managers need to avoid future undesirable changes in their salmon populations.

Acknowledgments

We thank J. Roos and J. Woodey of the International Pacific Salmon Fisheries Commission for providing the abundance and age structure data. Mart R. Gross and Brian Riddle contributed valuable suggestions. Funding was provided to the senior author by the Regional Planning Group of the Department of Fisheries and Oceans, Vancouver, B.C., by an operating grant from the Natural Sciences and Engineering Research Council of Canada, and by the National Research Council, Washington, DC. Facilities for completion of this research were kindly provided by the Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, CA.

References

BILTON, H. T. 1970. Maternal influences on the age at maturity of Skeena River sockeye salmon (*Oncorhynchus nerka*). Fish. Res. Board Can. Tech. Rep. 167: 20 p.

1971. A hypothesis of alternation of age of return in successive generations of Skeena River sockeye salmon (*Oncorhynchus nerka*). J.

Fish. Res. Board Can. 28: 513–516.

GARDNER, M. L. G. 1976. A review of factors which influence the sea-age and maturation of Atlantic salmon *Salmo salar L.* J. Fish Biol. 9: 289–327.

GJERDE, B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon *Salmo salar*. Aquaculture 38: 229–240.

GODFREY, H. 1958. A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. J. Fish. Res. Board Can. 15: 331–354.

GROSS, M. R. 1985. Disruptive selection for alternative life histories in salmon. Nature (Lond.) 313: 42–48.

HANSON, A. J., AND H. D. SMITH. 1967. Mate selection in a population of sockeye salmon (*Oncorhynchus nerka*) of mixed age groups. J. Fish. Res. Board Can. 24: 1955–1977.

HERSCHBERGER, W. K., R. N. IWAMOTO, AND A. M. SAXTON. 1982. Genetic potential for fresh- and seawater growth of net-pen cultured coho salmon, p. 185–192. *In* Proc. North Pac. Aquaculture Symp., Aug. 1980, Anchorage, AK.

INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION (IPSFC). 1978. Annual report for 1977, New Westminster, B.C.

KILLICK, S. R., AND W. A. CLEMENS. 1963. The age, sex ratio, and size of Fraser River sockeye salmon, 1915 to 1960. Int. Pac. Salmon Fish. Comm. Bull. XIV: 140 p.

LARKIN, P. A. 1971. Simulation studies of the Adams River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28: 1493–1502.

NAEVDAL, G. 1983. Genetic factors in connection with age at maturation. Aquaculture 33: 97–106.

NEAVE, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9: 450–491.

PETERMAN, R. M. 1985. Patterns of interannual variation in age at maturity of sockeye salmon (*Oncorhynchus nerka*) in Alaska and British Columbia. Can. J. Fish. Aquat. Sci. 42: 1595–1607.

PETERSON, A. E. 1954. The selective action of gillnets on Fraser River sockeye salmon. Int. Pac. Salmon Fish. Comm. Bull. V: 101 p.

REFSTIE, T. 1980. Genetic and environmental sources of variation in body weight and length of rainbow trout fingerlings. Aquaculture 19: 351–357.

REFSTIE, T., AND T. A. STEINE. 1978. Selection experiments with salmon. Part 3: Genetic and environmental sources of variation in length and weight of Atlantic salmon in the freshwater phase. Aquaculture 14: 221–234.

RICKER, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations, p. 19–160. *In* R. C. Simon and P. A. Larkin [ed.] The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C.

1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38: 1636–1656.

1982. Size and age of British Columbia sockeye salmon (*Oncorhynchus nerka*) in relation to environmental factors and the fishery. Can. Tech. Rep. Fish. Aquat. Sci. 1115: 117 p.

ROGERS, D. E. 1980. Density-dependent growth of Bristol Bay sockeye salmon, p. 267–283. *In* W. J. McNeil and D. C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

ROGERS, D. E., AND P. H. POE. 1984. Escapement goals for the Kvichak River system. Fish. Res. Inst., Univ. Washington, Seattle, WA, Publ. FRI-UW-8407: 66 p.

SAUNDERS, R. L., E. B. HENDERSON, B. D. GLEBE, AND E. J. LOUDENSLAGER. 1983. Evidence of a major environmental component in determination of the grilse: larger salmon ratio in Atlantic salmon (*Salmo salar*). Aquaculture 33: 107–118.

SUTTERLIN, A. M., AND D. A. MACLEAN. 1984. Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Can. J. Fish. Aquat. Sci. 41: 1139–1149.

THORPE, J. E., R. I. G. MORGAN, C. TALBOT, AND M. S. MILES. 1983. Inheritance of developmental rates in Atlantic salmon, *Salmo salar*. Aquaculture 33: 119–128.

TODD, I. ST. P., AND P. A. LARKIN. 1971. Gillnet selectivity on sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) of the Skeena River System, British Columbia. J. Fish. Res. Board Can. 28: 821–842.

VAN DEN BERGHE, E. P., AND M. R. GROSS. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 41: 204–206.

WARD, F. J., AND P. A. LARKIN. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. 11: 116 p.

Effects of Chronic Exposure to Sublethal pH on Growth, Egg Production, and Ovulation in Brook Trout, *Salvelinus fontinalis*

W. H. Tam and P. D. Payson

Department of Zoology, University of Western Ontario, London, Ont. N6A 5B7

Tam, W. H., and P. D. Payson. 1986. Effects of chronic exposure to sublethal pH on growth, egg production, and ovulation in brook trout, *Salvelinus fontinalis*. Can. J. Fish. Aquat. Sci. 43: 275–280.

Hatchery-reared brook trout (*Salvelinus fontinalis*) were maintained in the laboratory at mean pH values of 7.34, 5.56, 5.16, and 4.48 from early February to early December. At pH 4.48, the mean growth rates of males were uniformly lowered during the entire experimental period. Among females, growth was inhibited during the first 5 mo, but their rate of weight gain recovered during the period of rapid oocyte development. At the end of the experiment, the body weights of both male and female fish in pH 5.16 and 4.48 were only 70.70–77.34% of the control fish at pH 7.34. Growth was not affected by exposure to pH 5.56. Rapid oocyte development occurred simultaneously over all pH groups in June, suggesting that the initiation of gametogenesis was not affected over the range of pH tested. The number of eggs produced was significantly correlated to body weight; consequently the number of eggs produced by the smaller pH 5.16–4.48 females was reduced. Ovulation was also significantly delayed in the acidic groups.

Des ombles de fontaine (*Salvelinus fontinalis*) élevés en piscifacture ont été gardés au laboratoire à des pH moyens de 7,34, 5,56, 5,16 et 4,48, du début de février au début de décembre. À un pH de 4,48, le taux moyen de croissance des mâles a diminué de façon uniforme pendant toute la durée de l'expérience. Chez les femelles, il n'y a pas eu de croissance au cours des cinq premiers mois, mais elles ont recommencé à gagner du poids à un taux normal pendant la période de développement rapide des oocytes. À la fin de l'expérience, le poids des mâles et des femelles gardés à un pH de 5,16 et de 4,48 ne représentait que 70,70 à 77,34 % de celui des poissons témoins maintenus à un pH de 7,34. Un pH de 5,56 n'a pas eu d'effet sur la croissance. Les oocytes se sont développés rapidement en même temps pour tous les groupes soumis à des pH différents en juin, ce qui porte à croire que le début de la gamétogénèse n'a pas été affecté pour toute la gamme de pH vérifiés. On a établi de façon significative une corrélation entre le nombre d'oeufs produits et le poids corporel; par conséquent, le nombre d'oeufs produits par les femelles plus petites soumises à un pH de 5,16 et de 4,48 a été plus faible. L'ovulation a également été retardée de beaucoup chez les groupes soumis à des pH acides.

Received May 27, 1985
Accepted October 16, 1985
(J8257)

Reçu le 27 mai 1985
Accepté le 16 octobre 1985

Numerous reports have been made on the disappearance of fish populations as a result of lake acidification (see review by Haines 1981). The disappearance has been largely attributed to recruitment failure and not to the outright mortality of adults. Recruitment failure can be resolved into two components: inhibition of spawning (Beamish et al. 1975; Schofield 1976) and greater vulnerability of eggs and larvae to low pH than adults (Menendez 1976). Inhibition of spawning would imply the disturbance of reproductive processes such as gametogenesis and related endocrinology. Yet, very little is known about the changes in reproductive physiology of fish as the result of acidification of natural waters. The fact that certain metal concentrations increase concomitantly with decreasing pH (Wright and Gjessing 1976) necessitates the separate testing of these two factors to determine which is the cause of reproductive impairment. Our study investigated the effect of chronic exposure to sublethal pH alone on gonadal development, egg production, and ovulation in brook trout (*Salvelinus fontinalis*).

Materials and Methods

Brook Trout and Their Maintenance

Four hundred 11-mo-old brook trout (approximately 18 cm fork length and 100 g body weight) were purchased from Goossens Trout Farm (Otterville, Ont.) in December 1983. In the laboratory the trout were maintained in either 125 × 60 × 50 cm deep or 150 × 90 × 60 cm deep fibre glass tanks at approximately equivalent densities. The London, Ont., city water (pH 7.01–7.61; alkalinity TIP 78 mg/L; aluminum 0.095 mg/L, copper 0.003 mg/L) supplied to the tanks was dechlorinated to nondetectable levels (at the sensitivity limit of 0.02 mg total chlorine/L with a Hach Water Testing Kit (Hach Co., CO). The chlorine was removed by filtration through two activated charcoal filters (Flavr-Gard and Everpure T20, Culligan Water Conditioning Limited, London, Ont.) and then by 24-h aeration and mechanical agitation in a 1500-L capacity plastic tank. The water in the fish holding tanks was constantly aerated and recirculated through nylon

wool or a plastic sieve by magnetic drive pumps with plastic housings at the rate of 16–32 L/min before returning to the holding tanks. Because of the potential problems with metal dissolution by acidic water, plastic fittings and tubing were used to circulate water in the fish tanks. One third of the water was replaced daily and the tanks were cleaned monthly. All accessories needed for the management of the experimental fish were disinfected by immersion in hypochlorous acid solution when not in use. Water temperature was controlled by heat exchange with chilled water (3–6°C) circulated through coils of plastic tubing (15.24 m long × 1.2 cm i.d.). Water temperature was recorded several times a day (Table 1). The trout were fed once daily to near satiation with commercial trout food (Martin Feed Mills Limited, Elmira, Ont.). Tungsten and fluorescent lighting was controlled by electric timers (Paragon Electric Co., Guelph, Ont.) to mimic the natural photoperiod of 1984.

Trout were allowed 2 wk to acclimate to the water in the laboratory before they were divided into one neutral (group 1) and three acidic groups (groups 2, 3, and 4 with nominal pH of 5.5, 5.0, and 4.5, respectively) of equal size. Concentrated sulphuric acid (Baker Analyzed Reagent, J.T. Baker Chemical Co., Phillipsburg, NJ) was added to lower the pH in the acidic groups at intervals of 3–4 d first from neutral to pH 6.0 and then by 0.5 pH unit until the respective nominal pH was reached in early February 1984. After this initial period, pH was maintained by the addition of known amounts of sulphuric acid after the daily water change. During the remainder of the day, the target pH was maintained by dripping diluted sulphuric acid at known rates into the fish holding tanks with clinical intravenous infusion sets (Baxter Travenol Laboratories, Malton, Ont.). Actual pH was checked every 1–2 h from 08:30 to 18:00 daily (Table 1). Oxygen concentration was also checked periodically.

Mechanical failure and disease in June and August, respectively, interfered with the experiments. In June the water-filtration system in group 2 failed, resulting in some fish mortality. Only sufficient fish remained for sampling up to September; subsequently, this experimental group was terminated. In August, tail rot was first observed in some fish in group 3. Most of these fish were killed as the regular August samples. As a preventive measure the remaining fish of the group were treated with erythromycin (Erythrocin lactobinate; Abbott Laboratories Ltd., Montreal, Que.), on August 27 (11 mg/fish in 0.5 mL of 0.7% saline i.p.) and again on October 3, 1984 (11 mg/kg body weight in 0.7% saline i.p.), and periodically immersed for short durations in 2% potassium permanganate solution. All other brook trout exhibiting symptoms of tail rot were used as September samples, and thereafter, no more diseased fish were observed.

Sample Collection and Analysis

Approximately six males and six females from each experimental group were sacrificed during 8 of the 12-mo experimental period. The body weights and fork lengths were obtained. The gonads were dissected free of connective tissue, weighed, and fixed in 4CF-1G diagnostic fixative (McDowell and Trump 1976). From the first week of October to early December, the trout were checked daily to see if spermatozoa could be exuded and if ovulation had occurred by applying firm pressure on the abdominal cavity. If spermatozoa were present, a thin milt would be emitted from the genital pore. If ovulation had occurred, eggs would ooze freely out of the genital opening. After the female brook trout were sacrificed in November–December, 30–100 ovulated eggs were weighed, and from such weighings average egg weights were calculated for individual females. For females in which ovulation was judged to be recent or imminent from the size of the unovulated eggs and signs of breakdown of the ovarian wall, the total number of mature yolky eggs was counted.

The fixed ovaries were roughly divided into groups according to the extent of atresia. Atretic eggs were easily identifiable, as they became opaque following fixation. The number of healthy and atretic eggs in pairs of ovaries considered to be typical of each group was counted. These ovaries were then used as standards to visually estimate the percent of atretic eggs in every fish. Ovaries having less than 10% atretic eggs were rated as 1. The other scores were 2 for having 10–15%, 3 for 15–20%, 4 for 20–30%, and 10 for having 80–100% atretic eggs.

Analysis of variance (ANOVA) and Student–Newman–Keuls (SNK) a posteriori procedure were used to detect significant differences among body weight, body length, gonadosomatic index, average egg weight, and ovulation time. Where indicated, Student's *t*-test was also used to test for significant difference between a pair of means. The Kruskal–Wallis ranked ANOVA was used to detect significant differences in the extent of atresia between fish. Confidence limit was taken at the 5% level.

Results

Results are expressed as mean ±SE (number of observations or fish). Mean monthly temperatures and pH levels in groups 1 and 4 are given in Table 1 to illustrate the range of fluctuations throughout the experimental period. The overall mean pH values were pH 7.34 ± 0.01 (297) in group 1, pH 5.56 ± 0.02 (312) in group 2, pH 5.16 ± 0.03 (290) in group 3, and pH 4.48 ± 0.02 (292) in group 4. The actual pH values of groups 2–4 were therefore very close to their target values of pH 5.5, 5.0, and 4.5, and were significantly different from neutral and from one another (ANOVA, $p < 0.001$). The mean overall oxygen concentration was 6.9 ± 0.3(12) mg/mL with no apparent difference among the pH groups. Food consumption rate in all groups was about the same at 128.9 ± 5.6(30) g trout chow per 100 fish per day in March. Although the quantity of food was no longer accurately measured, no difference in food consumption was noticeable during the subsequent months. Throughout the experiments all fish mortalities appeared to be unrelated to pH exposure.

Somatic Growth

Body weights are given in Fig. 1. Within each pH group, body weight significantly increased during the experimental period (ANOVA, $p < 0.001$). Between-group comparison revealed that towards the latter half of the experimental period the mean body weight of the brook trout in group 4 was significantly lower (ANOVA, $p < 0.05$ to <0.001) than that of the fish in group 1 (control). The mean body weight of groups 2 and 3 were mostly between those of groups 1 and 4. At the end of the experiment, mean body weight of the males and females in group 4 was, respectively, 73.18 and 72.82% of the same sex in group 1. Regression lines were calculated for the females in groups 1 and 4 to cover the months when steady increase in

TABLE 1. Water temperature and pH of the neutral (group 1) and pH 4.48 (group 4) groups.

Month	Group 1		Group 2	
	Temperature (°C)	pH	Temperature (°C)	pH
Feb.	8.1±0.2	7.34±0.03	9.7±0.2	4.76±0.10
Mar.	7.9±0.1	7.40±0.02	8.8±0.1	4.50±0.06
Apr.	10.1±0.2	7.35±0.02	10.7±0.2	4.48±0.07
May	11.7±0.3	7.26±0.03	12.4±0.4	4.50±0.06
June	15.7±0.3	7.08±0.03	15.5±0.4	4.64±0.07
July	13.2±0.4	7.06±0.05	14.0±0.5	4.21±0.05
Aug.	11.9±0.2	7.36±0.04	11.6±0.2	4.42±0.05
Sept.	10.4±0.3	7.46±0.03	9.7±0.3	4.41±0.06
Oct.	9.2±0.2	7.55±0.03	8.5±0.2	4.59±0.06
Nov.	8.5±0.1	7.60±0.02	8.2±0.1	4.42±0.03

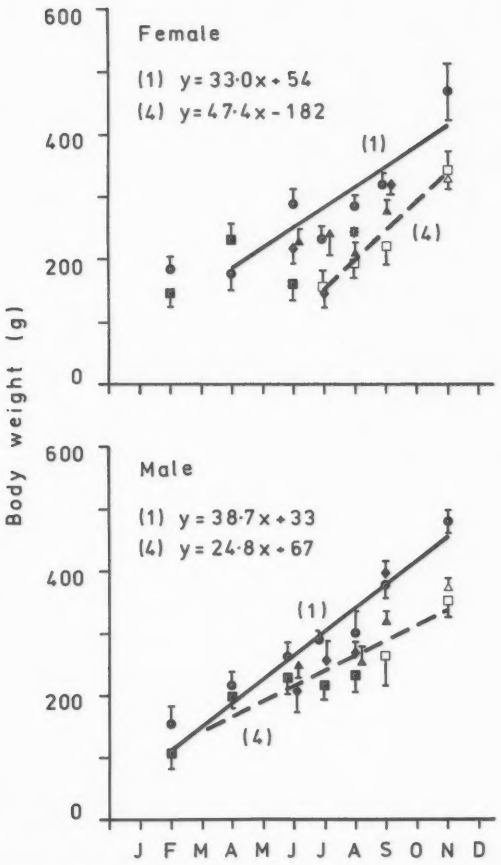


FIG. 1. Body weight of female and male brook trout obtained from Goossens Trout Farm and maintained in the laboratory (●, group 1; ◆, group 2; ▲, group 3; ■, group 4). Open symbols indicate significant difference (ANOVA) from control (group 1). Each point is the mean of 3–18 fish. The regression lines (1) and (4) are those of groups 1 and 4. Among the females, the regression lines cover the periods of April–November and July–November, and for the males February–November. The regression coefficients of the four lines are all significantly different from zero ($p < 0.001$).

body weight could be observed (Fig. 1). These were lines of similar slope with significantly different intercepts (Table 2). The regression lines of the males differed significantly from each other both in slope and intercept. There was no difference in slope and intercept between the males and females in group 1. However, between the males and females in group 4, both slope and intercept were significantly different from one another. The increase in fork length of the trout (Fig. 2) followed the same pattern as the changes in body weight throughout the experimental period.

Gonadal Growth, Egg Production, and Atresia

The gonado-somatic index (GSI) is the ratio of gonadal to body weight, expressed as milligrams per gram body weight (Fig. 3). In both males and females, there was no significant difference (ANOVA) between any group at any time of the experimental period. Gonadal weight began to increase in June and reached maximal values between September and November.

The mean ovulation times of the various groups are expressed relative to October 31, 1984 (day 0), to allow comparison (Table 3). Ovulation in groups 3 and 4 occurred very significantly later than group 1. No delay was observed in the males, as spermatozoa could be obtained from approximately 50% of the individuals in all groups by the end of October.

Correlation analysis showed that there was no correlation between body weight and the mean weight of the ovulated eggs in any experimental group. Thus, larger fish did not have larger eggs. There was also no significant difference in egg weight between the neutral and any of the acidic groups (Table 4). However, eggs from group 4 were significantly heavier than those of group 3 (ANOVA, $p < 0.02$). On the other hand, correlation and regression analyses showed that there was significant correlation between the total number of mature, yolky eggs and body weight in groups 1, 3, and 4 (Fig. 4). Further analysis showed that the regression lines of these groups did not differ in slope and intercept. When the data from all three groups were pooled, the number of eggs produced per female still increased in a linear fashion with increase in body weight (Fig. 4). Substituting the mean body weights (Fig. 1) obtained at the end of the experiment into this equation, the total numbers of yolky eggs produced by females having the mean body weight of each experimental group could be calculated (Table 4). The number of eggs produced in groups 3 and 4 only

TABLE 2. Regression analysis of changes in body weight in brook trout maintained at pH 7.34 (group 1) and pH 4.50 (group 4). NS = not significantly different.

	Slope			Intercept		
Group	Female	Male	p	Female	Male	p
1	33.0	38.7	NS	54	33	NS
4	47.4	24.8	<0.001	−182	67	<0.05
p	NS	<0.02		<0.001	<0.001	

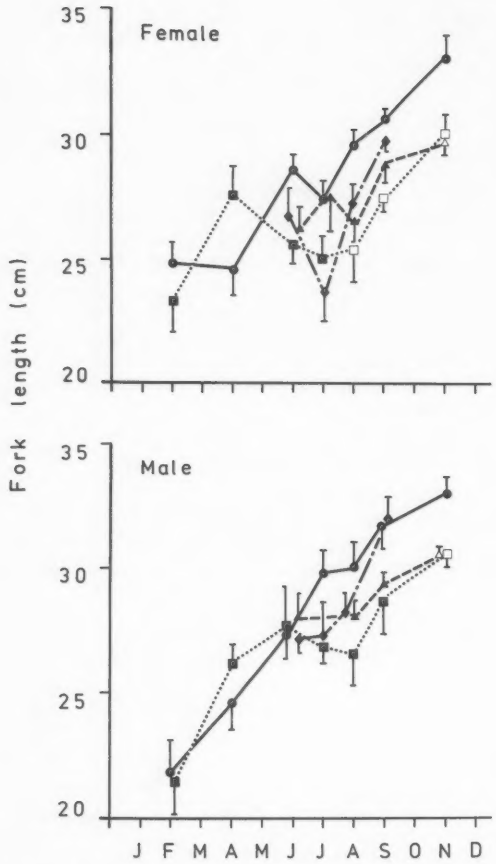


FIG. 2. Fork length of female and male brook trout obtained from Goossens Trout Farm (●, group 1; ◆, group 2; ▲, group 3; ■, group 4). Open symbols indicate significant difference (ANOVA) from control (group 1). Each point is the mean of 3−18 fish.

amounted to 63.86 and 66.49% of the neutral group.

The extent of atresia has been plotted in Fig. 5. The degree of atresia in groups 2 and 3 was significantly higher (ranked ANOVA, $p < 0.01$) than that of groups 1 and 4 in September. In November, only group 3 had more atretic eggs than groups 1 and 4 ($p = 0.004$).

Discussion

The outbreak of tail rot disease in group 3 during August and September aside, the trout in groups 1, 2, and 4 were healthy

TABLE 3. Mean ovulation time of the various experimental groups, expressed as number of days after October 31, 1984. The results are based on observations made on 34 females, all of which possessed mature, yolky eggs, and the experiment was terminated on December 14, 1984.

Group	pH	Proportion of fish ovulated	Ovulation time (days after October 31, 1984)[a]
1	7.34	3/4	14.3±0.3(3)
3	5.16	7/14	30.0±1.1(7)
4	4.48	11/16	19.6±0.8(8)

[a]Group 3 > group 4 > group 1, $p < 0.001$ (ANOVA).

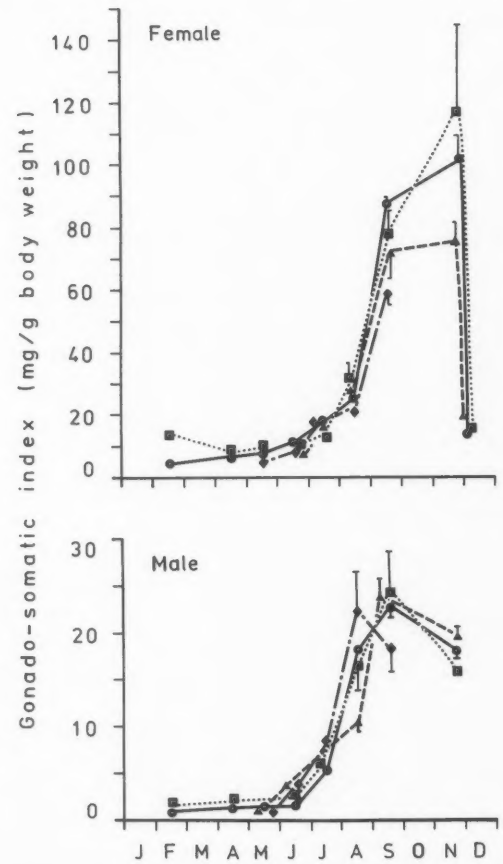


FIG. 3. Gonado-somatic index of female and male brook trout. Symbols and number of fish are the same as in Fig. 2.

TABLE 4. Average egg weight and the total number of eggs calculated for each female of average body weight at the end of the ovulation period.

Group	pH	Average female weight (g)	Average egg weight (mg)[a]	Number of eggs per female of average body weight[b]
1	7.34	471	29.8±2.7(7)	2020 (100.00)
3	5.16	333	27.6±2.1(8)	1290 (63.86)
4	4.48	343	33.3±1.1(13)	1343 (66.49)

[a]Group 1 was not significantly different from groups 3 and 4 (ANOVA).
[b]Number of eggs expressed as percent of those in group 1 in parentheses.

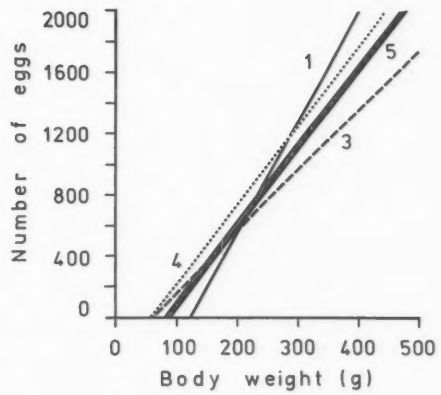


FIG. 4. Correlation between body weight and number of eggs produced per female. Line (1) = group 1, $y = 7.31x - 897$, $r^2 = 0.456$; line (3) = group 3, $y = 4.00x - 256$, $r^2 = 0.720$; line (4) = group 4, $y = 5.26x - 300$, $r^2 = 0.520$; line (5) = all groups combined, $y = 5.29x - 472$, $n = 50$, $r^2 = 0.403$.

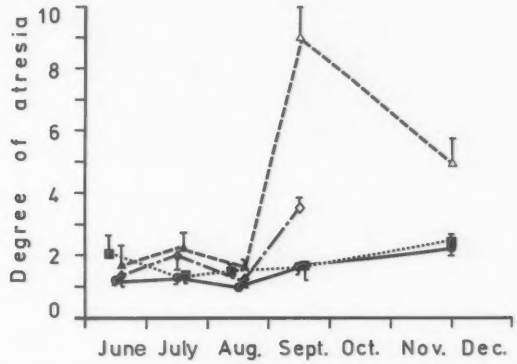


FIG. 5. Degree of atresia. Symbols are the same as in Fig. 2. Each point is the mean of 3–17 fish.

throughout the experiment. Even in group 3, tail rot did not cause a significant drop in body weight and length in August and September. Unlike most other studies in which fish were exposed to lowered pH, there was no mortality in this investigation that could not be traced to mechanical failure of the holding facilities. The summer temperature was suitable for growth and the autumn temperature was well within the range for proper development of gametes in brook trout (Hokanson et al. 1973). Metal concentrations were low compared with water in the lakes of northern Ontario (see water chemistry records of the Quality Protection Section, Ontario Ministry of the Environment). Oxygen concentration was high, and even at the high temperature experienced in June it should not limit active metabolism (Power 1980). Even though the growth of the control females appeared to be retarded in February–March, at the end of the experiment the body weight of the trout in the neutral pH was the same as those of the same age raised in the Goossens Trout Farm (Tam et al. 1985). The simultaneous retardation in the increase of body weight and length clearly indicated a suppression of growth in groups 3 and 4. The cause of growth inhibition can only be attributed to exposure to low pH. As the amounts of food consumed appeared to be the same, the retarded growth in groups 3 and 4 might have been due to disturbed metabolism. This is supported by reports that low pH has been identified as a stress that is responsible for elevated blood cortisol and glucose levels (Mazeaud et al. 1977; Brown et al. 1984). From the results of the regression analysis, the growth rates of male and female control fish were the same, and among the males, pH 4.48 uniformly suppressed growth from start to finish of the experiment. The females reacted to pH 4.48 in a very different way. Growth was retarded during the first 5 mo of exposure (February–July) but then recovered to a rate equal to that of the control fish, as suggested by the parallel regression lines. It is not clear why the female brook trout reacted differently from the males. The difference may possibly be related to the reproductive cycle, as recovery of growth occurred at the same time as the onset of the rapid phase of oocyte development and vitellogenesis (Tam et al. 1985).

Laboratory conditions did not appear to affect the reproductive biology of these brook trout, as gonadal development and oocyte production among the fish in group 1 were the same as those maintained in the Goossens Trout Farm (Tam et al. 1985). However, it appears that there were both indirect and direct effects of sublethally low pH on reproduction. Since in all cases GSI began to rise in June and at about the same rate, the initiation of gametogenesis was not delayed and the associated endocrine changes were therefore not impaired by low pH. In this experiment, as well as in another report (Vladykov 1956), the total number of eggs produced by brook trout could be significantly correlated with body weight. The suppression of body growth by low pH must result in lowering the total number of eggs produced by a fish population living below a certain pH level. We suggest that the reduction in egg production is an indirect consequence of retarded growth which is in turn due to the pathological metabolism that takes place when the animal is under acid stress. As the degree of atresia at pH 4.48 was not different from that of control, the atresia observed in group 3 (pH 5.16) was probably the result of stress imparted by tail rot. After the fish showing symptoms of the disease were eliminated in September the extent of atresia in the remaining

fish decreased dramatically in November. However, it is not known what caused the considerable degree of atresia in the group 2 fish during September. In some Ontario acidic lakes (pH 4.8–5.3), several fish species (Beamish et al. 1975) including brook trout (R. J. J. Roy, Department of Zoology, University of Western Ontario, London, Ont. N6A 5B7, pers. comm.) had been observed not to spawn even after their normal spawning period. This study shows that lowered pH is a direct cause of delayed ovulation in fish. Zischke et al. (1983) have previously shown delayed spawning in fathead minnows (*Pimephales promelas*) but offered no explanation for this delay. Sperm release was not retarded. Thus, low pH appears to adversely influence ovulation. The extensive delay in group 3 was probably a result of the combined stress of low pH and tail rot. The effects of lowered pH observed here were caused by chronic exposure to pH 5.16–4.48 for at least several months. The absence of effects at pH 5.56 shows the trout have at least some tolerance for acid conditions.

Acknowledgements

We gratefully acknowledge the financial support by a research contract (D.S.S. contract No. 20SU-31048-3-13644) from the National Research Council of Canada. We also thank Dr. R. J. J. Roy for his advice on statistical analysis.

References

BEAMISH, R. J., W. L. LOCKHART, J. C. VAN LOON, AND H. H. HARVEY. 1975. Long-term acidification of lake and resulting effects on fishes. Ambio 4: 98–102.

BROWN, S. B., J. G. EALES, R. E. EVANS, AND T. J. HARA. 1984. Interrenal, thyroid, and carbohydrate response of rainbow trout (*Salmo gairdneri*) to environment acidification. Can. J. Fish Aquat. Sci. 41: 36–45.

HAINES, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

HOKANSON, K. E. F., J. H. MCCORMICK, B. R. JONES, AND J. H. TUCKER. 1973. Thermal requirements for maturation, spawning, and embryo survival of the brook trout, *Salvelinus fontinalis*. J. Fish. Res. Board Can. 30: 975–984.

MAZEAUD, M. M., F. MAZEAUD, AND E. M. DONALDSON. 1977. Primary and secondary effects of stress in fish: some new data with a general review. Trans. Am. Fish. Soc. 106: 201–211.

MCDOWELL, E. M., AND B. F. TRUMP. 1976. Histologic fixatives suitable for diagnostic light and electron microscopy. Arch. Pathol. Lab. Med. 100: 405–414.

MENENDEZ, R. 1976. Chronic effects of reduced pH on brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 118–123.

POWER, G. 1980. The brook charr, *Salvelinus fontinalis*, p. 141–203. *In* E.K. Balon [ed.] Salmonid fishes of the genus *Salvelinus*. Vol. 1. Charrs. Dr. W. Junk bv Publishers, The Hague, The Netherlands.

SCHOFIELD, C. L. 1976. Acid precipitation: effects on fish. Ambio 5: 228–230.

TAM, W. H., R. J. J. ROY, AND R. MAKARAN. 1985. Ovarian cycle and plasma concentrations of estrogen and vitellogenin in brook trout (*Salvelinus fontinalis*, Mitchill). Can. J. Zool. 63. (In press)

VLADYKOV, V. D. 1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. J. Fish. Res. Board Can. 13: 799–841.

WRIGHT, R. F., AND E. T. GJESSING. 1976. Changes in the chemical composition of lakes. Ambio 5: 219–223.

ZISCHKE, J. A., J. W. ARTHUR, K. J. NORDLIE, R. O. HERMANUTZ, D. A. STANDEN, AND T. P. HENDRY. 1983. Acidification effects on macroinvertebrates and fathead minnows (*Pimephales promelas*) in outdoor experimental channels. Water Res. 17: 47–63.

Changes in Mean Weight, Sea-Age Composition, and Catch-per-Unit-Effort of Atlantic Salmon (*Salmo salar*) Angled in the Godbout River, Quebec, 1859–1983

Alex T. Bielak

Atlantic Salmon Federation, Suite 1030, 1435 St-Alexandre, Montreal, Que. H3A 2G4

and Geoffrey Power

Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1

Bielak, A. T., and G. Power. 1986. Changes in mean weight, sea-age composition, and catch-per-unit-effort of Atlantic salmon (*Salmo salar*) angled in the Godbout River, Quebec, 1859–1983. Can. J. Fish. Aquat. Sci. 43: 281–287.

A weight-age classification, based on recent catches, was retroactively applied to angled Atlantic salmon (*Salmo salar*) catches recorded in the log of the Godbout salmon club between 1859 and 1983. Over this period, numbers of salmon caught have fluctuated with a periodicity of 20–30 yr but catches have been maintained. There has been a big increase in fishing effort, and the proportion of two-sea-year to previously spawned fish has increased. The mean weight of these age groups has declined 0.005–0.009 kg·yr^{-1}. These changes are attributed to the selective effects of commercial fisheries on the stock.

Une classification par poids et âge basée sur les prises récentes a été appliquée aux données de prise de la pêche sportive du saumon de l'Atlantique (*Salmo salar*) enregistrées par le club de pêche du saumon de la rivière Godbout entre 1859 et 1983. Au cours de cette période, le nombre de saumons capturés a fluctué selon une périodicité de 20 à 30 ans, mais les prises se sont maintenues. Il y a eu une importante augmentation de l'effort de pêche et la proportion des poissons ayant passé deux ans en mer par rapport aux poissons ayant déjà frayé s'est accrue. Le poids moyen de ces groupes d'âge s'est abaisse de 0,005–0,009 kg·an^{-1}. Les auteurs attribuent cette variation aux effets sélectifs de la pêche commerciale de ce stock.

Received January 24, 1985
Accepted October 16, 1985
(J8077)

Reçu le 24 janvier 1985
Accepté le 16 octobre 1985

There is a great deal of anecdotal information which suggests that changes have occurred in size and age of Atlantic salmon (*Salmo salar*) in many rivers throughout its range. Porter et al. (1986) in one of the synthesis papers for the Salmonid Age-at-Maturity Workshop specifically identified the serious lack of time series of information on characteristics of individual wild stocks.

This study examines the historical catch record of salmon by anglers on the Godbout River (about 50°N, 68°W) of the Quebec North Shore to determine if changes have taken place in catch composition and age-specific mean weight of the stock. Trends in numbers of fish angled and catch-per-unit-effort (CPUE) are also examined over the period of the record.

Materials and Methods

Historical Salmon Catch Record

The 124-yr records of the Godbout Club, dating back to 1859, are probably the longest and most complete chronicle of salmon fishing in North America. In addition to providing immaculately kept salmon weight records, the fishing logs facilitate quantification of effort; historically, a 09:00–17:00 fishing day prevailed at the club, and it is thus possible to establish the number of man-days of fishing per season, as well as number of anglers participating. Measures of CPUE of various age-classes of salmon could also be calculated for the last 120 yr. Unfortunately, as with most clubs prior to the time salmon became scarcer, grilse (one-sea-year salmon) were not considered worth recording consistently (members and guides of North Shore angling clubs, pers. comm.). Although noted for some seasons between 1859 and 1900, they were not recorded at all for the next 60 yr. Even now, individual grilse weights are noted rather infrequently.

Data Analysis

The fishing records of the Godbout Club provide individual fish weights in pounds and the date on which fish were taken for most years between 1859 and 1983. A weight–frequency distribution of fish of known age, from collections made by Schiefer (1971) and Bielak (1984), was used to group fish into the following age-specific weight classes: (a) grilse, less than 5.0 lb (2.3 kg); (b) two-sea-year salmon, greater or equal to 5 lb and less than or equal to 14.0 lb (6.4 kg); (c) previous spawners and three-sea-year salmon, greater than 14 lb. Of 186 fish, 100% of grilse and the previously spawned – three-sea-year groups (N = 34 and 11, respectively) and 95.3% of two-

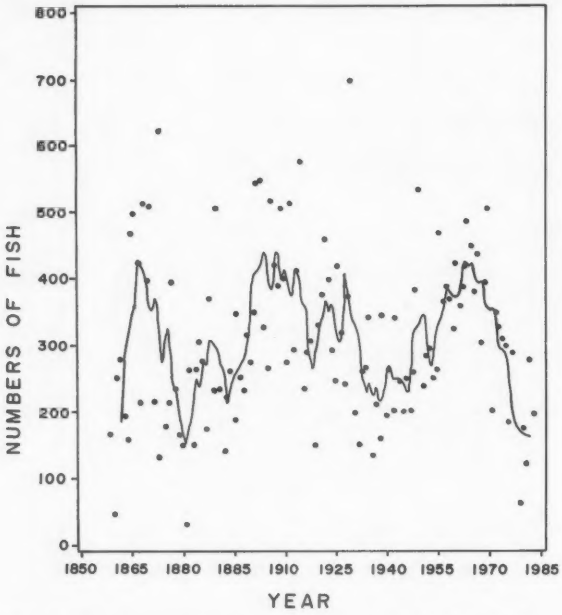


FIG. 1. Catches of large salmon (excluding grilse) by the Godbout Fishing Club, 1859–1983. The line shows the 5-yr moving average of numbers of salmon caught.

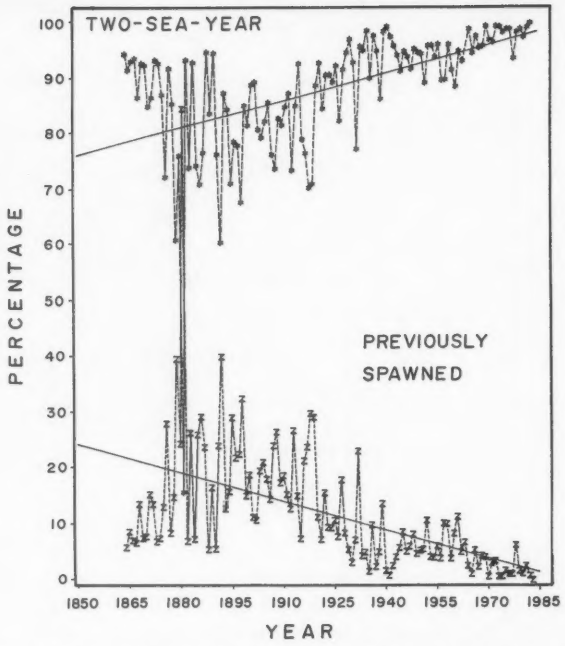


FIG. 2. Relative proportions of two-sea-year and previously spawned salmon, 1864–1983; catches of the Godbout Fishing Club (grilse excluded).

sea-year salmon ($N = 141$) were correctly classified by weight. The high classification success and our experience with other historical North Shore data sets indicate that these limits are appropriate. Of the 11 fish in the previously spawned – three-sea-year category, 10 were previous spawners, and this class is therefore referred to in the text as previously spawned. No fish in this group had spawned for the first time as grilse.

The weight age conversion and classification was then retroactively applied to fish recorded in the club log books. The conversion of weight to age makes inference possible regarding temporal changes in (1) the proportion of the run made up by each sea-age-class and (2) the mean weight of the fish of each class.

Temporal trends in stock characteristics were analysed by plotting (1) percentages of total catch occurring in each sea-age-class and (2) the mean weight of fish in each class. The variance of the percentage was used to weight the linear regression to account for different catches between years. Regressions of mean weight with time were weighted by the number of fish in each class. Regression coefficients for slope (b) were tested (H_0: $b = 0$) using a t-test. All tests were done at the 5% probability level. For comparative purposes, analyses were carried out, both for the full period and from 1963 on, when grilse, whether kept or released, began to be regularly recorded. To test for a relationship between grilse taken in one year, and two-sea-year salmon taken the next, the actual number of fish taken in year ($n + 1$) were regressed on the number of fish taken in year (n).

Uncertainties in analyses of historical records include questions about the accuracy of weights, completeness of records, bias towards larger fish or portions of the run, and the validity of retroactive classification in the face of possible changes in mean weight. These difficulties have been thoroughly discussed by Riley et al. (1984) and Bielak (1984). The comprehensive nature of the records and details of fishing practices at the Godbout Club mitigates most of these problems.

Results

Regression Analyses — Temporal Trends

1859–1983

There has been no consistent change in the total catch of large salmon by the Godbout Club for the period examined (Fig. 1). There does, however, appear to be an oscillation, with a period of between 20 and 30 yr between periods of high catches. When grilse are excluded from the analysis, because of sporadic early recording, proportions of two-sea-year salmon increase and previously spawned decrease relative to each other (Fig. 2). It is notable that the large early deviations from a line of best fit diminish substantially in later years (Table 1 shows levels of significance and r^2 values for regressions referred to in text).

Age-specific mean weights (Fig. 3) declined significantly ($p = 0.0001$) (0.005 and 0.009 kg·yr^{-1} and 0.01 and 0.02 lb·yr^{-1}, respectively, for two-sea-year and previously spawned salmon). Mean weight of all large salmon, which is of such importance to anglers as a general indicator, also declined with time ($p = 0.0001$).

1963–1983

There was no significant trend in catches of either grilse or larger salmon (Fig. 4). Previously spawned fish show a barely significant ($p = 0.04$) decline. When grilse are excluded from the analysis, the decline in previously spawned relative to two-sea-year salmon is more highly significant ($p = 0.0003$). For

TABLE 1. Results of regression analyses on proportions and weights of Godbout River salmon angling catch. *Significant at $p < 0.05$; ***significant at $p < 0.001$.

Data series	Test category	Probability (p) (slope = 0)	Coefficient of determination (r^2)	Slope	Intercept
1864–1983	% two-sea-year salmon	0.61	0.002		
	% previous spawners	0.0001***	0.49	−0.11	228.67
	% two-sea-year salmon (excluding grilse)[a]	0.0001***	0.41	0.11	−122.86
	% previous spawners (excluding grilse)	0.0001***	0.41	−0.1	222.86
	Mean weight total catch	0.0001***	0.64	−0.018	38.00
	Mean weight two-sea-year salmon	0.0001***	0.45	−0.005	15.98
	Mean weight previous spawners	0.0001***	0.37	−0.009	25.58
	Mean weight multi-sea-year salmon (excluding grilse)	0.0001***	0.49	−0.014	27.13
1963–83	% grilse	0.31	0.06		
	% two-sea-year salmon	0.35	0.04		
	% previous spawners	0.04*	0.21	−0.07	5.92
	% two-sea-year salmon (excluding grilse)	0.0003***	0.52	0.12	89.98
	% previous spawners (excluding grilse)	0.0003***	0.52	−0.12	10.02
	Mean weight total catch	0.53	0.02		
	Mean weight two-sea-year salmon	0.02*	0.25	0.018	2.72
	Mean weight previous spawners	0.21	0.09		
	Mean weight multi-sea-year salmon (excluding grilse)	0.09	0.15		

[a]Test category (excluding grilse) involves use of all data except records of fish <2.3 kg weight.

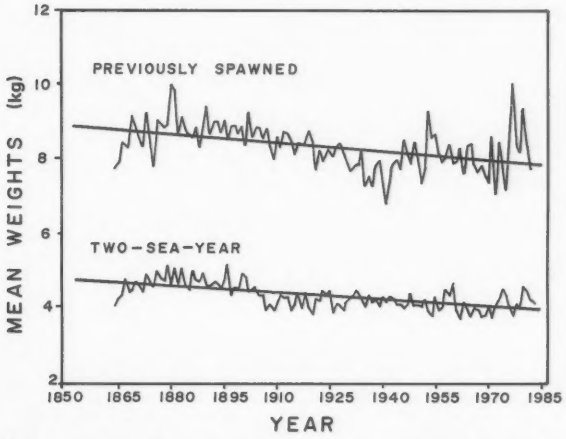


FIG. 3. Age-specific mean weights of two-sea-year and previously spawned salmon in the catch of the Godbout Fishing Club, 1864–1983.

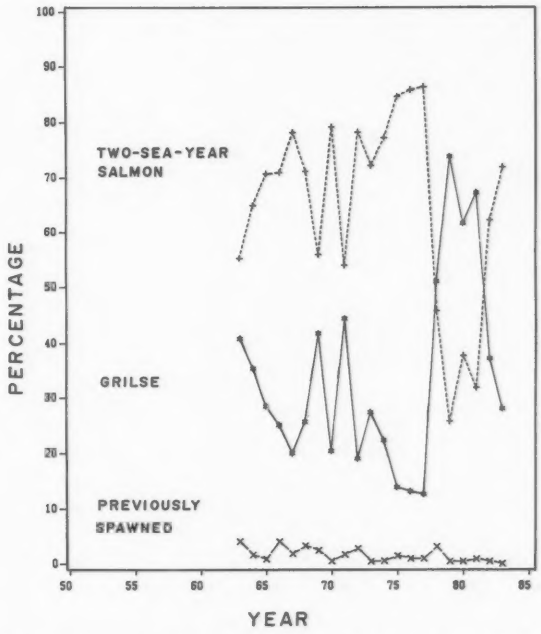


FIG. 4. Proportions of the various sea-ages of salmon caught by the Godbout Fishing Club, 1963–83.

this shorter period, age-specific mean weight rose in two-sea-year salmon, but not for previously spawned fish. The increase is significant ($p = 0.02$) but the r^2 value for the regression is relatively low. Mean weight of total catch, whether including or excluding grilse, does not change significantly over the period.

There is a significant ($0.05 > p > 0.02$) correlation between grilse taken in any particular year and two-sea-year salmon taken the following year. Such an analysis could not be undertaken for the period 1859–1983 because of the lack of sufficient grilse records.

Fishing effort

Increases in length of the fishing season, number of fishermen, and fishing effort are particularly evident since the mid-1950's (Fig. 5). As fishing effort increases, the number of grilse taken increases sharply (Fig. 6A). This increase is most evident at effort levels of over 180 man-days. Such effort levels have only been common in the last 25 yr (see Fig. 5C).

Numbers of two-sea-year salmon caught can be interpreted as rising initially, but tending to level off as effort increases

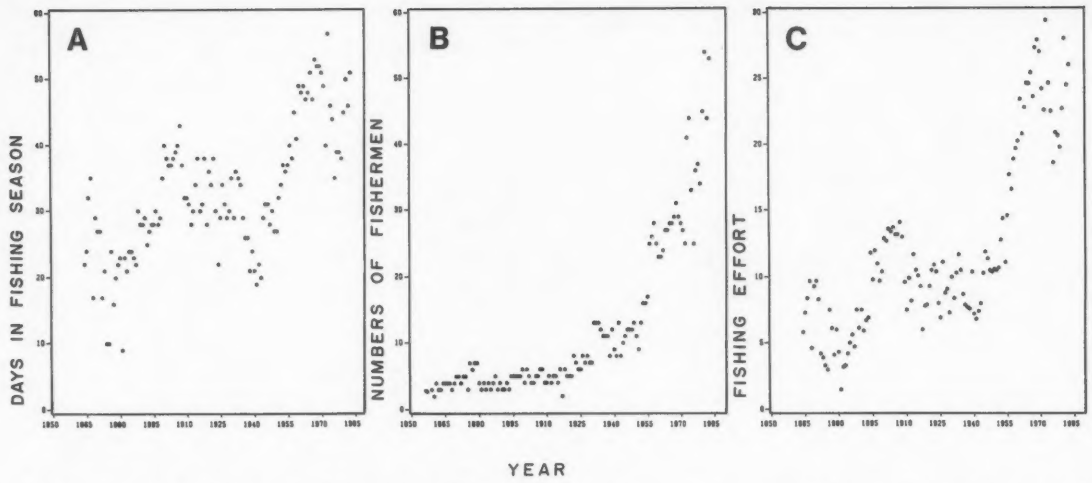


FIG. 5. Fishing effort in the Godbout River. (A) Days in the fishing season (1864–1983); (B) numbers of fishermen (1859–1983); (C) fishing effort in 10 angler-day units (1864–1983).

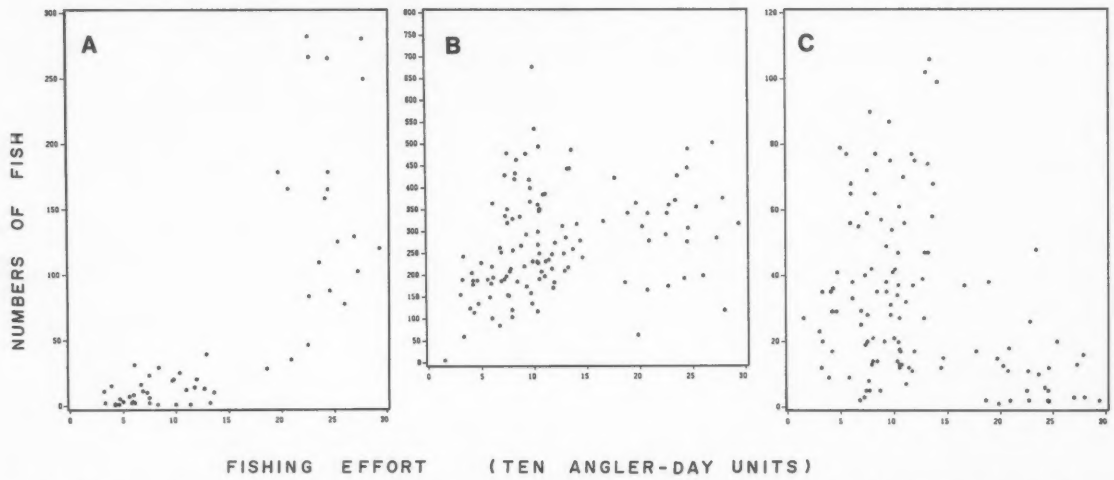


FIG. 6. Catches of (A) grilse, (B) two-sea-year, and (C) previously spawned salmon plotted against fishing effort, Godbout Fishing Club records, 1864–1983.

(Fig. 6B). Numbers of previously spawned caught (Fig. 6C) show no trend whatsoever where effort was below 180 man-days, i.e. the period prior to 1955. Generally, fewer previous spawners were taken in years of highest effort, a time by which the proportion and number of fish in this class had already fallen substantially (see Fig. 2).

Severe declines in catch per man-day of fishing of two-sea-year and previously spawned salmon have occurred (Fig. 7). In both cases the wide scatter, about a line of best fit, of points for the early years should be noted, as should the decrease in such scatter in recent years.

Discussion

Long-term Atlantic salmon catch records are often unavailable or incomplete. Statistics dealing with catches in a specific area (e.g. the Maritimes, Huntsman 1931; Canada and Scotland, Menzies 1951; the Baltic, Lindroth 1965; Newfoundland and Labrador, Taylor 1985) are often restricted to total number or weight of fish landed in commercial fisheries. Records of angling and commercial catches within particular rivers are often similar in this respect and are rarely comprehensive (e.g. Berg 1964; Power 1976). The fullest analysis, prior to this study, of a long-term (72 yr) record is that for the River Wye (U.K.) by Gee and Milner (1980).

Analyses of more recent, and generally shorter term, records usually include reports of trends in relative abundance of constituent age-classes. Analyses range from anecdotal (e.g. Chadwick et al. 1978) to studies with restricted statistical treatment of data (e.g. Thorpe and Mitchell 1981; Kristjánsson 1983; Riley et al. 1984). Most studies simply discuss trends (e.g. Belding 1938; Porter and Finn 1983) or show them graph-

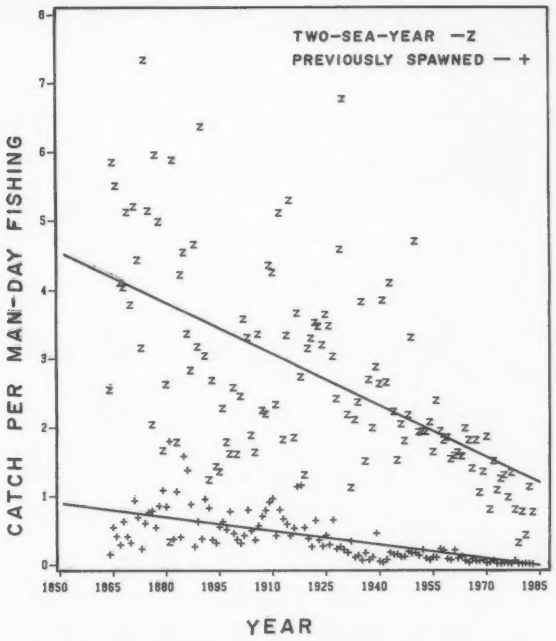


FIG. 7. Catch per fishing day of two-sea-year and previously spawned salmon, Godbout Fishing Club records, 1864–1983.

ically (e.g. Schiefer 1971; Ruggles and Turner 1973). It is in this context that the importance of the Godbout records becomes apparent; apart from the changes observed in the stock and its exploitation, it is evident that only over the longer term can such trends be discerned. It is also clear that analysis of historical records should not be divorced from popular or eyewitness accounts of the fishery. The sporadic early records of grilse in the Godbout, and their apparent plentitude after 1963, would probably have been addressed in a biological context had not the far simpler explanation, discussed previously, surfaced in the course of background interviews with long-time members and staff from this, and other, camps.

There is no consistent change in angling catch (excluding grilse) of the Godbout Club (Fig. 1), although fishing effort has increased substantially over the years (Fig. 5). The very dramatic decreases in CPUE of large salmon (Fig. 7) indicate that increasing numbers of anglers are competing for either a stable or declining number of fish. The relative long-term stability of total harvest, together with the indication that catch of two-sea-year salmon may level out with increasing effort (Fig. 6B), suggests that all the fish available to be caught are in fact being taken. This conclusion is supported by the obvious decreasing scatter about the trend lines in Fig. 7; in the early years more salmon were probably available, and the number which might be taken could be large or small, presumably depending on angling conditions, number of fishermen, season length, etc. More recently, the scatter has decreased, indicating that the number of fish to be taken is smaller, and that all fish are taken subject, to a far lesser extent than previously noted, to angling conditions. The decline in CPUE is proportionately greater for previous spawners (approximately 10-fold) than for two-sea-year fish (approximately 5-fold).

Yearly fluctuations in the relative proportions of different sea-age-classes returning to spawn have been described for various salmon stocks (Schiefer 1971; Gee and Milner 1980), and Mills (1971) cited studies by many authorities reporting biological cycles of abundance of varying periodicities. Such fluctuations make it difficult to detect real trends in short-term data sets. This is illustrated by the much lower r^2 values reported for regressions on the shorter of the two Godbout data sets (Table 1), and by the near-absence of highly significant results, when compared with the longer term analysis. It is clear that important changes have occurred in the ratio of two-sea-year salmon to previously spawned fish, and that these are most highly significant in the long-term data.

One may conclude that the ratios of grilse to larger salmon have not changed, in the short term at least. Increases in the ratio of grilse to larger salmon have been reported for the Miramichi (New Brunswick) (Saunders 1969; Ruggles and Turner 1973), Western Arm Brook (Newfoundland) (Chadwick et al. 1978), and Matamek (Quebec) (Gibson 1978; Gibson and Côté 1982) rivers. Results for the Matamek are equivocal because Whoriskey and Naiman (1982) reported no evident change in the ratio of grilse to larger salmon for that river. Commercial catches of grilse in Scotland rose between 1952 and 1976 and landings of larger salmon declined (Department of Agriculture and Fisheries for Scotland 1981; Martin and Mitchell, cited in Thorpe et al. 1981). However, little change in the proportion of large salmon from Icelandic rivers is reported (Kristjánsson 1983; Scarnecchia 1983).

It is debatable whether any shifts in the ratio of Godbout grilse to larger salmon would become evident if complete long-term data were available for study. Our assessment is that any changes are more apparent than real, if one takes into account (1) the spasmodic early records of substantial grilse catches, (2) the early stigma associated with keeping grilse when one could catch larger salmon, and (3) the trend to increased fishing pressure and longer seasons which would tend to increase grilse catches.

The higher rate of decline in weight of previously spawned relative to two-sea-year salmon is predictable, since almost all previously spawned fish returned initially as two-sea-year salmon. Decreases in mean weight of total catch are due to a combination of the effects described above, i.e. (1) decreases in the proportion of previously spawned fish, (2) decreases in age-specific mean weights, (3) fishing season extension resulting in higher grilse catches, and (4) recent consistent recording of grilse.

The low, but significant, correlation ($r = 0.27$) between grilse catch and two-sea-year salmon catch the following year suggests that factors at sea are influencing eventual riverine catches in the Godbout. A perfect correlation would indicate no differential mortality (or other effect) acting at sea on those age-classes. Kristjánsson (1983) showed very high correlations ($r = 0.80–0.99$) for three Icelandic rivers, but far weaker ones for others (no r values reported). He explained the good correlations by suggesting commercial fisheries (and/or natural mortality) had had a minor impact on the populations of the three rivers. The corollary is that if no correlations were evident, factors at sea would be entirely responsible for the lack of a relationship.

The changes and/or relationships described above for the Godbout appear uniformly directed, and have also been noted in other North Shore rivers (Bielak 1984). It is therefore unlikely that they have been randomly generated. Factors that could be responsible include natural changes to, and human

impact on, biological and physical environments, and direct human influence through various fisheries.

The Quebec North Shore is generally regarded as a near-pristine environment where salmon are moderately exploited in the rivers by angling, some native subsistence fishing, and poaching. Since there is no evidence, for the North Shore, of changes in river discharge or in precipitation cycles in recent years (Naiman 1980, 1982) nor in precipitation patterns over a long period (Canadian A.E.S. long-term records), it seems unlikely that climatic factors have affected the freshwater phase. Therefore, the only plausible factors which might consistently have acted over the last century, or more, to produce the changes described must almost certainly relate to changes in the natural marine environment or to fisheries of various kinds, especially commercial fisheries exploitation at sea.

Salmon abundance and life history patterns may change in response to oceanic temperature (Saunders et al. 1983; Scarnecchia 1983, 1984; Martin and Mitchell, cited in Thorpe and Mitchell 1981). Indeed, the change and subsequent reversal in the ratio of grilse to two-sea-year salmon shown in Fig. 4 is probably best explained by environmental influences. The same explanation may apply to some of the relatively high previously spawned weights in the last decade (Fig. 3); however, some of those points are based on comparatively small sample numbers because of the decline in the incidence of this age-class (Fig. 2). Although evidence has been presented on long-term variations in marine conditions in the northwest Atlantic which have affected salmon distribution (Dunbar and Thomson 1979), there are none which might correlate with the directed age-specific mean weight and stock composition changes reported in this study. Periods of warming and cooling have occurred (Dunbar 1982; Longley, cited in Thomas 1975) but the duration and magnitude of the trends are unlikely to be the cause of the long-term changes observed in the Godbout. Variations in availability of food organisms also seem unlikely to be a strong selective force over an extended period given the plasticity of the salmon's diet (see Scott and Crossman 1979).

The only sustained selective force which might engender such changes is that of commercial fisheries acting on stocks in the marine environment. Fisheries prosecution of North Shore salmon was extensively dealt with by Bielak (1984). He concluded, from the various studies he examined, that both distant and local commercial fisheries exploitation was historically severe (e.g. Comeau 1923; Belding and Prefontaine 1938, 1961; Huard 1972; Gibson and Côté 1982; Bastien 1984), and continues to be important, with heaviest pressure probably on multi-sea-year salmon (e.g. Murray 1968; Saunders 1969). It was not feasible, however, to establish exploitation levels or rates for Godbout salmon over time.

Changes in *both* proportions of age-classes and age-specific mean weights have not been previously documented for Atlantic salmon. They probably reflect unquantified, long-standing selection pressures on adult fish by commercial fisheries. Ricker (1981) comprehensively discussed various potential causes and effects of life history changes in five species of Pacific salmon; for chinook salmon (*Oncorhynchus tshawytscha*), he considered the two major causes of change to be fisheries induced and to have a genetic basis, i.e. (1) a change in the genetic basis of age-at-maturity with increased representation of younger fish among breeding individuals, because larger (hence older) fish are taken in commercial fisheries, and (2) a change in the genetic basis of growth rate due to selection of larger fish of any given age by the fishery. He also dealt with the differential capture of multi-sea-winter fish over grilse.

Schaffer and Elson (1975) and particularly Handford et al. (1977) addressed the evolutionary implications of such selection. The former authors suggested that commercial exploitation had selectively altered the frequencies of genes coding for different ages of return among North American salmon populations. Handford et al. (1977) reported many studies which gave evidence that growth rate is heritable to some degree, and concluded that growth rates will usually respond fairly rapidly to selection.

We suggest that Ricker's (1981) conclusions, as detailed above, are likely to hold for Atlantic salmon. Therefore, future studies of Atlantic salmon might profitably address the question of sustained changes in frequencies of genes coding for fast growth or different ages at first return. They should also investigate year-to-year fluctuations in stock composition and age-specific mean weight in relation to fluctuations in the marine environment because all of the above have important implications with respect to the future value and yields of Atlantic salmon fisheries.

Acknowledgements

This work was supported by a NATO science scholarship to A.T.B., an NSERC operating grant to G.P., and grants from the Atlantic Salmon Association and Woods Hole Oceanographic Institution. We thank members and staff of the Godbout Fishing Club, who allowed us access to valuable club records and collected data on recent catches, and Michael Huband, who helped us interpret the records and gave freely of his knowledge of the club's history. Thoughtful reviews by R. L. Saunders and an anonymous reviewer improved the manuscript.

References

BASTIEN, Y. 1984. A study of the interception of mainland origin Atlantic salmon in the Newfoundland commercial fishery. Report for the Atlantic Salmon Federation. 32 p. (Available from Atlantic Salmon Federation, St. Andrews, N.B.)

BELDING, D. L. 1938. The salmon of the Moisie River. Trans. Am. Fish. Soc. 67: 195–206.

BELDING, D. L., AND G. PREFONTAINE. 1938. Studies on the Atlantic salmon: II. Report on the salmon of the 1937 Port-aux-Basques (Newfoundland) drift-net fishery. Contrib. Inst. Zool. Univ. Montréal No. 3: 58 p.

1961. A report on the salmon of the North Shore of the Gulf of St. Lawrence and the northeastern coast of Newfoundland. Contrib. Dep. Fish. Prov. Que. No. 82: 104 p.

BERG, M. 1964. Nord-Norske Lakseelver, Oslo: Johan Grundt Tanum Forlag. 300 p.

BIELAK, A. T. 1984. Quebec North Shore Atlantic salmon stocks. Ph.D. dissertation, University of Waterloo, Waterloo, Ont. 236 p.

CHADWICK, E. M. P., T. R. PORTER, AND P. DOWNTON. 1978. Analysis of growth of Atlantic salmon (*Salmo salar*) in a small Newfoundland river. J. Fish. Res. Board Can. 35: 60–68.

COMEAU, N. A. 1923. Life and sport on the North Shore. 2nd ed. Quebec Telegraph Printing Co. 440 p.

DEPARTMENT OF AGRICULTURE AND FISHERIES FOR SCOTLAND. 1981. Triennial review of research, 1976–1978. Freshwater Fisheries Laboratory, Pitlochry, Scotland. 70 p.

DUNBAR, M. J. 1982. Twentieth century marine climatic change in the northwest Atlantic and subarctic regions. NAFO Sci. Counc. Stud. 5: 7–15.

DUNBAR, M. J., AND D. H. THOMSON. 1979. West Greenland salmon and climatic change. Medd. Grønl. 202(4): 19 p.

GEE, A. S., AND N. J. MILNER. 1980. Analysis of 70-year catch statistics for Atlantic salmon (*Salmo salar*) in the River Wye and implications for management of stocks. J. Appl. Ecol. 17: 41–57.

GIBSON, R. J. 1978. Recent changes in the population of juvenile Atlantic salmon in the Matamek River, Quebec, Canada. J. Cons. Int. Explor. Mer 38(2): 201–207.

GIBSON, R. J. 1978. Recent changes in the population of juvenile Atlantic salmon in the Matamek River, Quebec, Canada. J. Cons. Int. Explor. Mer 38(2): 201–207.

GIBSON, R. J., AND Y. CÔTÉ. 1982. Production de saumonneaux et recaptures de saumons adultes étiquetés à la rivière Matamec, Côte-Nord, Golfe du Saint-Laurent, Québec. Naturaliste can. (Rev. Ecol. Syst.) 109: 13–25.

HANDFORD, P., G. BELL, AND T. REIMCHEN. 1977. A gill net fishery considered as an experiment in artificial selection. J. Fish. Res. Board Can. 34: 954–961.

HUARD, V. A. 1972. Labrador et Anticosti. Re-edition of original 1897 text by Editions Lemeac Inc., Montreal, Que. 505 p.

HUNTSMAN, A. G. 1931. The maritime salmon of Canada. Biol. Board Can. Bull. 21: 99 p.

KRISTJÁNSSON, J. 1983. An observation on fishing records of some salmon rivers of the northeast and eastern areas, 1969–1981. (Translation from Icelandic by Multilingual Services Division, Department of the Secretary of State of Canada. From Veithimathurinn, p. 39–44 (undated). 13 p. typescript)

LINDROTH, A. 1965. The Baltic salmon stock. Mitt. Int. Ver. Limnol. 13: 163–192.

MENZIES, W. J. M. 1951. A report on the present position of the Atlantic salmon fisheries of Canada with recommendations for their regulation and improvement. Atl. Salmon Assoc. Doc. No. 17: 40 p.

MILLS, D. 1971. Salmon and trout: a resource, its ecology, conservation and management. Oliver and Boyd, Edinburgh. 351 p.

MURRAY, A. R. 1968. Smolt survival and adult utilization of Little Codroy River, Newfoundland, Atlantic salmon. J. Fish. Res. Board Can. 25: 2165–2218.

NAIMAN, R. J. 1980. Matamek Annual Report for 1979. Woods Hole Oceanogr. Inst. Tech. Rep. WHOI-80-31: 270 p.

1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. The Matamek Research Program: Annual Report for 1981. Woods Hole Oceanogr. Inst. Tech. Rep. WHOI-82-29: 12–43.

PORTER, R., AND J. FINN. 1983. Are there fewer salmon in the river on the Avalon today than there were 25 years ago? The Salmon Association of Eastern Newfoundland. Salar Alert Newslett. No. 5: 4 p.

PORTER, T. R., AND M. C. HEALEY (WITH E. T. BAUM, A. T. BIELAK, Y. CÔTÉ, AND M. F. O'CONNELL). 1986. Implications of varying the sea-age at maturity of Atlantic salmon (*Salmo salar*) on yield to fisheries. Can. Spec. Publ. Fish. Aquat. Sci. (In press)

POWER, G. 1976. History of the Hudson's Bay Company salmon fisheries in the Ungava Bay region. Polar Rec. 18(113): 151–161.

RICKER, W. E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38: 1636–1656.

RILEY, S. C., A. T. BIELAK, AND G. POWER. 1984. The Atlantic salmon stock of the Grand Watshishou River, Quebec: a historical perspective. Naturaliste can. 111(3): 219–228.

RUGGLES, C. P., AND G. E. TURNER. 1973. Recent changes in stock composition of Atlantic salmon (*Salmo salar*) in the Miramichi River, New Brunswick. J. Fish. Res. Board Can. 39: 779–786.

SAUNDERS, R. L. 1969. Contributions of salmon from the Northwest Miramichi River, New Brunswick, to various fisheries. J. Fish. Res. Board Can. 26: 269–278.

SAUNDERS, R. L., E. B. HENDERSON, B. D. GLEBE, AND E. J. LOUDENSLAGER. 1983. Evidence of a major environmental component in determination of the grilse:larger salmon ratio in Atlantic salmon (*Salmo salar*). Aquaculture 33: 107–118.

SCARNECCHIA, D. L. 1983. Age at maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 40: 1456–1468.

1984. Climate and oceanic variations affecting yields of Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 41: 917–935.

SCHAFFER, W. M., AND P. F. ELSON. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56: 577–590.

SCHIEFER, K. 1971. Ecology of Atlantic salmon, with special reference to occurrence and abundance of grilse, in North Shore Gulf of St. Lawrence rivers. Ph.D. dissertation, University of Waterloo, Waterloo, Ont. 129 p.

SCOTT, W. B., AND E. J. CROSSMAN. 1979. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. (3rd ed.) 184: 966 p.

TAYLOR, V. R. 1985. The early Atlantic salmon fishery in Newfoundland and Labrador. Can. Spec. Publ. Fish. Aquat. Sci. 76: 71 p.

THOMAS, M. K. 1975. Meteorological studies of climatic fluctuations in Canada 1917–1960. An annotated bibliography. DS 7/75 Environment Canada. Climatology Div. A.E.S., Toronto, Ont. 9 p.

THORPE, J. E., AND J. F. KOONCE (WITH D. BORGESON, B. HENDERSON, A. LAMSA, P. S. MAITLAND, M. A. ROSS, R. C. SIMON, AND C. WALTERS). 1981. Assessing and managing man's impact on fish genetic resources. Can. J. Fish. Aquat. Sci. 38: 1899–1907.

THORPE, J. E., AND K. A. MITCHELL. 1981. Stocks of Atlantic salmon (*Salmo salar*) in Britain and Ireland: discreteness and current management. Can. J. Fish. Aquat. Sci. 38: 1576–1590.

WHORISKEY, F. G., AND R. NAIMAN. 1982. Effects of commercial fishing on adult Atlantic salmon (*Salmo salar*) in a Quebec river. Woods Hole Oceanogr. Inst. Tech. Rep. WHOI-82-2: 17 p.

Lake Acidification as a Limiting Factor in the Distribution of the Freshwater Amphipod *Hyalella azteca*

M. Stephenson and G. L. Mackie

Department of Zoology, University of Guelph, Guelph, Ont. N1G 2W1

Stephenson, M., and G. L. Mackie. 1986. Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca*. Can. J. Fish. Aquat. Sci. 43: 288–292.

The distribution of the freshwater amphipod *Hyalella azteca* in 79 Ontario lakes suggests that its absence may be a good indicator of lake acidification. *Hyalella azteca* was present in 69 of 71 nonacidified lakes, and absent in 8 of 8 lakes which either are now ar recently were considered acidified. Bioassay data indicate a 96-h LC_{50} of pH 4.4 and a 10-d threshold LC_{50} of pH 4.5 for *H. azteca* in a natural surface water. *Hyalella azteca* is extremely rare in Plastic Lake, which undergoes severe short-term acidification in spring, and recruitment is delayed 2 wk in Heeney Lake which undergoes similar short-term acidification. In Dickie, Harp, Red Chalk, and Blue Chalk lakes, where springtime pH depressions below pH 4.7 were not recorded, *H. azteca* is abundant.

La distribution de l'amphipode d'eaux douces *Hyalella azteca* dans 79 lacs de l'Ontario porte à croire que son absence peut être un bon indice de l'acidification des lacs. *H. azteca* était présent dans 69 des 71 lacs non acidifiés et absent de 8 lacs acidifiés depuis plus ou moins longtemps. Des essais biologiques ont permis de déterminer une CL_{50} de 96 h à pH 4,4 et une CL_{50} seuil de 10 jours à pH 4,5 pour *H. azteca* en eaux de surface naturelles. Cet organisme est extrêmement rare dans le lac Plastic qui subit une importante acidification de courte durée au printemps, et le recrutement est décalé de 2 sem dans le lac Heeney qui subit lui aussi une acidification du même type. L'espèce est cependant abondante dans les lacs Dickie, Harp, Red Chalk et Blue Chalk, où l'on n'a pas noté de baisse printanière du pH inférieure à pH 4,7.

Received June 6, 1985
Accepted October 21, 1985
(J8284)

Reçu le 6 juin 1985
Accepté le 21 octobre 1985

The freshwater amphipod *Hyalella azteca* is widely distributed in North America. Bousfield (1958) reported its habitats to include lakes, ponds, sloughs, marshes, estuaries, rivers, streams, ditches, and spring streams from Mexico north to the tree line in Canada and Alaska, and from Atlantic to Pacific, with the sole proviso that monthly mean summer water temperatures must exceed 10°C. *Hyalella azteca* is the only North American representative of its genus and is the most common and widely distributed North American freshwater amphipod. It is an important food item for young game and forage fish (Cooper 1965) and plays a significant role in cropping periphyton production (Hargrave 1970). The elimination of *H. azteca* through lake acidification would clearly constitute a substantial biological impact.

European workers have found a number of benthic macroinvertebrates that are sensitive to acidification (Raddum and Fjellheim 1984). Okland (1980) and Okland and Okland (1980) reported that the amphipod *Gammarus lacustris* tolerates acidification to pH 6.0 in cold lakes and to pH 6.6 in warmer lakes. Other organisms (including the isopod *Asellus*, snails, and pisidiid clams) were shown to have somewhat greater tolerances to acidification, and were proposed as organisms having indicator potential for different stages in the process of acidification.

In North America, the benthic community received relatively little attention in acid-rain related research. Roff and Kwiatkowski (1977) showed a decline in benthic diversity with declining pH in the La Cloche region of Ontario, which implies the elimination or exclusion of sensitive species, and Collins et al. (1980) reported that snails were excluded at low pH in the same area. Benthic organisms having indicator potential, however, have not been identified.

Here we report on the distribution of *H. azteca* in Ontario lakes sensitive to acidification, the abundance of *H. azteca* in six lakes near Dorset, Ontario, which range from moderate to extreme sensitivity to acidification, and bioassay data comparing the observed sensitivity of *H. azteca* to hydrogen ion toxicity with observed springtime pH minima.

Methods

In July and August 1984, 79 lakes between Sudbury and Kingston, Ontario, were sampled. A list of these lakes, their locations, presence/absence of *H. azteca*, and measured alkalinity is available upon request. Up to 30 min was spent at one site on each lake by two investigators (60 search min) searching for *H. azteca*. The sampling technique used involved raking surficial sediments with a scoop-like sieve (0.40-mm opening) and sorting the sieved sediment for *H. azteca* on the spot. If *H. azteca* was found, it was usually found within the first 5 min of searching. Animals captured were held alive in lake water and kept cool until their identity could be confirmed.

Surface water samples were taken in 500-mL plastic bottles

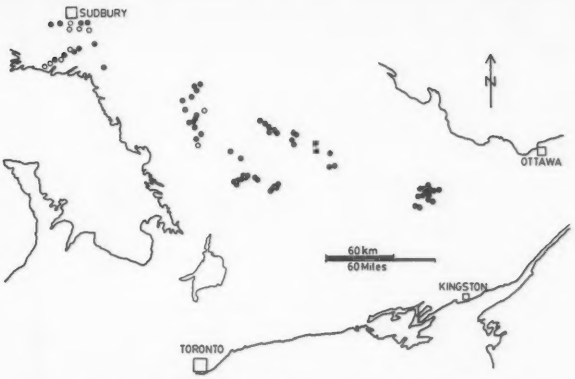


FIG. 1. Presence (solid points) or absence (open points) of *Hyalella azteca* in 79 surveyed Ontario lakes.

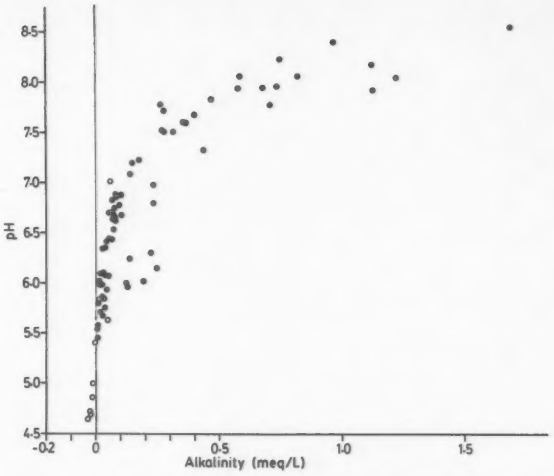


FIG. 2. Presence (solid points) or absence (open points) of *Hyalella azteca* indicated on a plot of pH versus alkalinity for lakes in Ontario, surveyed in late summer, 1984. The vertical line indicates zero alkalinity.

for pH and alkalinity determination. Bottles were acid washed and then thoroughly rinsed and filled with distilled water. On site they were emptied and then rinsed three times with lake water before being filled. Air bubbles were excluded. Samples were kept in the dark, on ice to minimize biological effects, and were analyzed within 24 h of collection. A Fisher Accumet 144 pH meter equipped with a combination pH electrode, standardized before use with pH 7.00 and pH 4.00 buffers, was used for determination and alkalinity titrations. Total inflexion point alkalinity was determined using a Gran titration and a computer regression programme.

Between June 1983 and May 1984, *H. azteca* populations in six lakes (Plastic, Heeney, Dickie, Harp, Blue Chalk, and Red Chalk) near Dorset, Ontario, were studied. Samples were taken every 2 wk in the summer, and less frequently in the fall and winter. *Hyalella azteca* was sampled in each lake by randomly taking 15 cores (5 cm depth, 7.62 cm diameter) in shallow (<1.0 m) water at specific sites in each lake. Sediments were sieved in the field with a 0.40-mm-opening sieve and kept cool until hand sorted, usually within 24 h. No mortality was observed before sorting. Animals collected were kept frozen in distilled water until they could be counted.

Immediately before the benthic samples were taken, two replicate surface water samples were taken for pH and alkalinity measurement as previously described. Bottles were dedicated to each site and were simply rinsed with distilled water between sampling periods.

A bioassay was conducted in duplicate to determine the toxicity of hydrogen ions to *H. azteca* in a natural surface water (from Dickie Lake, near Dorset: Ca^{2+}, 2.71 mg/L; Mg^{2+}, 0.63 mg/L; Na^{+}, 0.85 mg/L; DOC, 4.6 mg/L). The test was a static bioassay at 4°C, with a 12 h light : 12 h dark photoperiod. *Hyalella azteca* was collected in December 1984 from Harp Lake. The animals were assumed to be winter acclimated, as the lake already had full ice cover and the water temperature was 2°C. Sediment collected was transported back to the laboratory where the animals were sorted and held in lake water at 4°C until used. Ten animals were used in each replicate at each pH level tested (pH 5.6, 5.2, 5.0, 4.7, 4.5, and 4.2). The experimental tanks were 1.0-L polyethylene containers with lids. These had been detergent washed, rinsed in deionized water, soaked in dilute acid (pH 2.0), and rinsed with distilled water prior to use. The experimental pH levels were established and stable before the amphipods were added. The animals were starved for 24 h prior to, and for the duration of, the bioassay. The number of animals living in each treatment was recorded at 3, 6, 12, 24, 36, 48, 60, 72, 84, and 96 h and daily thereafter for a total of 10 d to determine a threshold LC_{50}. The experimental pH was measured and adjusted by addition of dilute (0.01 *M*) H_2SO_4 on a daily basis or as needed. The desired pH was usually maintained within 0.05 pH unit, and always within 0.10 pH unit. Death was defined as the failure of an animal to respond to gentle prodding, and the absence of a heartbeat. Probit analysis was used to determine an LC_{50} for each time at which there was greater than 50% mortality in any treatment.

Results

Hyalella azteca was present in only about half of the Sudbury area lakes, while it was present in almost all of the lakes sampled in other areas of Ontario (Fig. 1). When the presence or absence of *H. azteca* is indicated on a plot of pH versus alkalinity (Fig. 2), a clear pattern emerges. *Hyalella azteca* is totally absent from lakes with a negative epilimnetic summertime alkalinity (acidified lakes) and is present in all but four of those lakes sampled having a positive alkalinity. These four lakes are all considered to be sensitive to acidification (alkalinity <0.1 meq/L).

Mean population densities of *H. azteca* in the Dorset area lakes in 1983 are plotted against time in Fig. 3. In Plastic Lake, the only animals found were subadult and adult animals recruited the previous year. In Heeney Lake, recruitment did not begin until after July 7, and there was no consistent increase in population densities during the summer months. In Dickie, Red Chalk, Blue Chalk, and Harp lakes, recruitment began in late June, and population densities increased exponentially until late August, when recruitment ceased.

The results of the bioassay are summarized as a toxicity curve (Fig. 4). For *H. azteca*, a 96-h LC_{50} for hydrogen ions in Dickie Lake water was calculated to be 4.15×10^{-5} *M* (pH 4.4). A threshold LC_{50} value was calculated to be about pH 4.5 at 10 d.

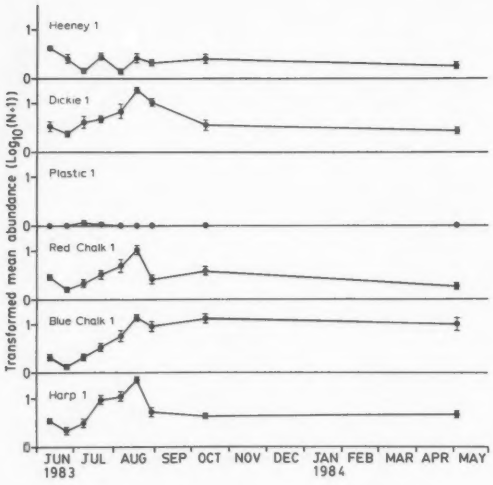


FIG. 3. Population densities ($\log_{10}(N + 1)$) of *Hyalella azteca* recovered from core samples (15 on each sampling date in each lake) from lakes in the Dorset area. Vertical bars indicate ±1 standard error of the mean. Core size was 45.6 cm^2.

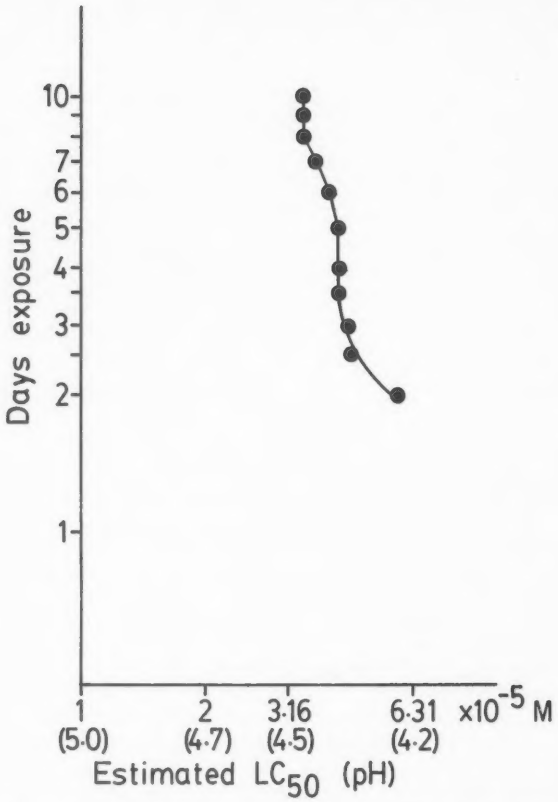


FIG. 4. Toxicity curve plotting LC_{50}'s for hydrogen ions to *Hyalella azteca* against time. A 96-h LC_{50} was estimated to be 4.15×10^{-5} mol H^+/L (pH 4.4), and a 10-d threshold LC_{50} was estimated as equivalent to pH 4.5.

Discussion

Hyalella azteca appears to have been eliminated from Sudbury area lakes with summertime epilimnetic alkalinities of less than zero. Two of the four nonacidified lakes from which *H. azteca* was absent are Sudbury area lakes (George Lake, Killarney Twp.; Raft Lake, Dill and Broder Twps.) which are historically documented as being acidified (Ontario Ministry of the Environment 1978), but which have shown increased epilimnetic pH and buffering capacity since cuts in Sudbury nickel production and SO_2 emissions. The third nonacidified lake that lacked *H.azteca* was Sollman Lake in the Magnetawan region. Sollman Lake, in addition to having low pH and alkalinity (pH 5.83, alkalinity 0.031 meq/L), had the lowest concentrations of Ca^{2+} (1.42 mg/L), Mg^{2+} (0.31 mg/L), and SO_4^{2-} (3.41 mg/L) recorded in this survey. Since freshwater amphipods are hyperosmotic to their environment, and hemolymph concentrations of these ions are strongly regulated (Mantel and Farmer 1983), it is possible that one or more cations, probably calcium, are present in Sollman Lake at a lower than limiting concentration. The fourth lake that lacked *H. azteca* was Dill Lake, Dill Twp., near Sudbury. Dill Lake has no documented history of acidification, and the present survey recorded no unusual water chemistry. Therefore, either *H. azteca* is present in Dill Lake, but was not detected by this survey, or *H. azteca* is absent from Dill Lake for unknown reasons. Thus, *H. azteca* was found in 69 of 71 lakes with a positive alkalinity and none of 8 lakes which either are now or historically were acidified.

Because the most severely acidified lakes encountered were in the Sudbury area, and because those lakes receive large atmospheric inputs of heavy metals (Cu, Ni, Zn, and Fe) (Jeffries and Snyder 1981), acidification per se cannot immediately be called a limiting factor in the distribution of *H. azteca*. The distribution of *H. azteca* in Ontario lakes may be affected by (i) acidification (hydrogen ion toxicity, or toxicity due to changed speciation of normal levels of heavy metals) or (ii) by elevated levels of heavy metals, or aluminum.

Population studies on *H. azteca* from six Dorset area lakes suggest that acidification may be the limiting factor. In the four best-buffered Dorset area lakes studied (mean summertime epilimnetic alkalinities of Blue Chalk, Red Chalk, Harp, and Dickie lakes in 1983: 0.0955, 0.0836, 0.0800, and 0.0147 meq/L, respectively), recruitment begins in late June, and population growth is exponential (linear when transformed by $\log_{10}(N + 1)$) for the entire recruitment period between late June and late August. Lindeman and Momot (1983) recorded a similar recruitment period in Dock Lake near Thunder Bay, Ontario. In Heeney lake (mean summertime epilimnetic alkalinity in 1983 of 0.0071 meq/L) the population appeared stressed, with the onset of recruitment being delayed about 2 wk (reducing the recruitment period to only 6 wk), and population densities did not increase consistently during the summer. In Plastic Lake (mean summertime epilimnetic alkalinity in 1983 of 0.0017 meq/L), no recruitment was observed and population densities were extremely low. The Dorset area lakes do not have the elevated inputs of heavy metals associated with lakes in the Sudbury area (Jeffries and Snyder 1981), yet *H. azteca* populations become increasingly stressed and display anomalous reproductive patterns as pH levels approach those (pH 5.6, alkalinity 0.0000 meq/L) suggested by the survey of

(pH 5.6, alkalinity 0.0000 meq/L) suggested by the survey of lakes across Ontario. Therefore, high concentrations of heavy metals in the water column can be rejected as agents causing the decline of *H. azteca* populations. Similarly, Brehm and Meijering (1982) concluded that although the mobilization of heavy metal ions can increase the toxicity of waters to the amphipods *Gammarus pulex* and *G. fossarum*, mortality is mainly due to the increasing concentration of free hydrogen ions.

Although Dorset area lakes do not show abnormally high levels of heavy metals, aluminum concentrations can become elevated during periods of high runoff (LaZerte 1984), and fish kills in Plastic Lake have been attributed to aluminum toxicity (Harvey and Lee 1982). While aluminum may be highly toxic to some animals at some life history stages (Muniz and Leivestad 1980; Baker and Schofield 1982), it appears to be harmless or even therapeutic to *H. azteca*, at low pH. G. L. Mackie and C. Soto (unpubl. data) found that levels of inorganic monomeric aluminum between 50 and 400 μg/L resulted in almost 100% survival of *H. azteca* at pH 4.2, while lower levels of aluminum (<4 μg/L) resulted in 100% mortality at pH 4.2 after 96 h. Presumably this is related to ionic exchange processes involved with acid–base balance. Positive ions (especially Na^+ from the external environment) are exchanged for hydrogen ions from the hemolymph at the gill surface. Excess hydrogen ions in the external environment compete with sodium for binding sites, making Na^+ uptake and H^+ excretion difficult (Havas 1980). High concentrations of other cations have a similar effect (Leivestad et al. 1976; Jozuka and Adachi 1979). It is possible that high concentrations of Al^{3+} help reduce hydrogen ion stress by reducing their effective concentration in the external environment.

The bioassay data show that exposure of *H. azteca* to pH below 4.50 in a natural surface water may cause significant mortality. In Plastic and Heeney lakes, surface waters analyzed in early May 1984 had a pH of less than 4.50. The lowest pH recorded in Dickie Lake was 4.70, and Red Chalk, Blue Chalk, and Harp lakes all maintained pH levels above 5.00. Thus, there is potential for acute toxicity due to hydrogen ion stress in populations of *H. azteca* in Plastic and Heeney lakes.

It seems likely, then, that *H. azteca* is eliminated from lakes when they undergo long-term acidification and that hydrogen ion stress is the most important limiting factor. Population failure may be due to acute toxicity during the spring or fall runoff periods when pH and alkalinity are depressed, or due to recruitment failure caused by long-term exposure to low (but not lethal) pH. Although the survey data indicate a fairly sharp limit of pH 5.6 (zero alkalinity), there may be some variability in the precise pH or alkalinity level at which *H. azteca* is eliminated, related to the concentration of cations (Na^+, K^+, Ca^{2+}, and Mg^{2+}) in solution. Since most Ontario lakes susceptible to acidification are very dilute, this source of variation will probably not be significant in most cases. Factors that might increase the persistence of *H. azteca* populations in acidifying lakes include high NaCl or $CaCl_2$ inputs from road salting or wetting operations or salt inputs from ocean aerosols in coastal areas.

These results suggest that *H. azteca* has potential as an indicator of lake acidification. As an indicator, *H. azteca* is not as sensitive as *G. lacustris* in Europe, which is eliminated at a very early stage of acidification (Okland 1980; Okland and Okland 1980), while *H. azteca* is not eliminated until the onset of long-term acidification. Although the distribution of *H. azteca* may also be limited by other factors (such as extremely low concentrations of Ca^{2+}), its absence from a lake sensitive to acidification is sufficient evidence to suggest that acidification may be having a substantial biological impact. *Hyalella azteca* can be collected without specialized equipment (waders and fine sieve are all that is necessary), and it is easily identified (with the aid of a dissecting microscope). It should find application as an indicator organism in regional surveys of lake acidification status and as an indicator of the deterioration of sensitive lakes over a period of years.

Acknowledgements

We thank Dr. P. J. Dillon of the Ontario Ministry of the Environment for providing water chemistry analysis for the 1984 survey of lakes. R. Turland, J. Carbone, B. Muncaster, and L. McLeod helped with laboratory and field work. M. Stephenson was supported in part by an Ontario Graduate Scholarship and a Xerox Scholarship. The study was supported by NSERC strategic grant No. G0918 to G. L. Mackie.

References

BAKER, J. P., AND C. L. SCHOFIELD. 1982. Aluminum toxicity to fish in acidic waters. Water Air Soil Pollut. 18: 289–309.

BOUSFIELD, E. L. 1958. Fresh-water amphipod crustaceans of glaciated North America. Can. Field-Nat. 72: 55–113.

BREHM, J., AND M. P. D. MEIJERING. 1982. On the sensitivity to low pH of some selected crustaceans (*Daphnia* and *Gammarus*, Crustacea). Arch. Hydrobiol. 95: 17–27.

COLLINS, N. C., A. P. ZIMMERMAN, AND R. KNOECHEL. 1980. Comparisons of benthic infauna and epifauna biomasses in acidified and non-acidified Ontario lakes, p. 35–48. *In* R. Singer [ed.] Effects of acidic precipitation on benthos. North American Benthological Society, Colgate University, Hamilton, NY.

COOPER, W. E. 1965. Dynamics and production of a natural population of a fresh-water amphipod, *Hyalella azteca*. Ecol. Monogr. 35: 377–394.

HARGRAVE, B. T. 1970. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnol. Oceanogr. 15: 21–30.

HARVEY, H. H., AND C. LEE. 1982. Historical fisheries changes related to surface water pH changes in Canada, p. 45–55. *In* R. E. Johnson [ed.] Acid rain/Fisheries. American Fisheries Society, Bethesda, MD.

HAVAS, M. 1980. Physiological response of aquatic animals to low pH, p. 49–65. *In* R. Singer [ed.] Effects of acidic precipitation on benthos. North American Benthological Society, Colgate University, Hamilton, NY.

JEFFRIES, D. S., AND W. R. SNYDER. 1981. Atmospheric deposition of heavy metals in central Ontario. Water Air Soil Pollut. 15: 127–152.

JOZUKA, K., AND H. ADACHI. 1979. Environmental physiology on the pH tolerance of teleost: I. Some inorganic factors affecting the survival of medaka, *Oryzias latipes*, exposed to low pH environment. Jpn. J. Ecol. 29: 221–228.

LAZERTE, B. D. 1984. Forms of aqueous aluminum in acidified catchments of central Ontario: a methodological analysis. Can. J. Fish. Aquat. Sci. 41: 766–776.

LEIVESTAD, H., G. HENDREY, I. P. MUNIZ, AND E. SNEKVIK. 1976. Effects of acid precipitation on freshwater organism, p. 86–111. *In* F. H. Braekke [ed.] Impact of acid precipitation on forest and freshwater ecosystems in Norway. Research Rep. 6/76, SNSF project, Oslo-As, Norway.

LINDEMAN, D. H., AND W. T. MOMOT. 1983. Production of the amphipod *Hyalella azteca* (Sassure) in a northern Ontario lake. Can. J. Zool. 61: 2051–3059.

MANTEL, L. H., AND L. L. FARMER. 1983. Osmotic and ionic regulation, p. 53–162. *In* L. H. Mantel [ed.] The biology of Crustacea 5. Internal anatomy and physiological regulation. Academic Press, New York, NY.

MUNIZ, I. P., AND H. LEIVESTAD. 1980. Acidification — effects on freshwater fish, p. 84–92. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. SNSF project, Oslo-As, Norway.

OKLAND, K. A. 1980. Mussels and crustaceans: studies of 1,000 lakes in Norway, p. 324–325. *In* D. Drablos and A. Tollan [ed.] Ecological

impact of acid precipitation. SNSF project, Oslo-As, Norway.

OKLAND, J., AND K. A. OKLAND. 1980. pH level and food organisms for fish: studies of 1,000 lakes in Norway, p. 326–327. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. SNSF project, Oslo-As, Norway.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1978, Sudbury environmental study report: extensive monitoring of lakes in the greater Sudbury area 1974–1976. Ontario Ministry of the environment, Toronto, Ont.

RADDUM, G. G., AND A. FJELLHEIM. 1984. Acidification and early warning organisms in freshwater in western Norway. Verh. Int. Ver. Limnol. 22: 1973–1980.

ROFF, J. C., AND R. E. KWIATKOWSKI. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

Introduction: Phosphorus–Plankton Dynamics Symposium[1]

Stephen J. Tarapchak

Great Lakes Environmental Research Laboratory, 2300 Washtenaw Avenue, Ann Arbor, MI 48104, USA

and Czesia Nalewajko

Life Sciences Division, Scarborough Campus, University of Toronto, Military Trail, West Hill, Toronto, Ont. M1C 1A4

Phosphorus–plankton dynamics is a scientifically challenging, continuously evolving discipline. Research historically has focused on the role of P as a limiting factor in primary and secondary production. Extensive efforts have been made to understand the eutrophication process, model P-limited phytoplankton growth, predict the outcome of species competition, and understand the regenerative mechanisms that resupply orthophosphate (P_i) to algae. Research on P in the Great Lakes has focused primarily on water quality monitoring programs and the use of P budget models to predict future changes in trophic state. However, to model production dynamics in the Great Lakes system accurately, studies on P cycling are urgently required. The P–Plankton Dynamics Symposium, composed of an international group of scientists working in marine and in freshwater systems, was convened to examine our current understanding of the field. To introduce the symposium papers, we briefly trace the development of scientific investigation into cultural eutrophication, identify major research themes and problems in P–plankton dynamics and in P cycling, and summarize basic and applied research on eutrophication and P cycling in the Great Lakes.

Cultural Eutrophication

The causes and consequences of cultural lake eutrophication have been recognized as a practical and scientific problem for over 50 yr (NAS 1969; Thomas 1973; Vallentyne 1974). Studies on P–plankton dynamics are rooted in the early attempts to understand the causes of phytoplankton blooms. For example, Einsele's (1941) classic study on the fertilization of Schleinsee with superphosphates initiated the era of whole-lake enrichment experiments. Similarly, Sawyer (1947) detected that blooms in the Madison lakes, Wisconsin, were largest in lakes receiving the greatest quantities of N and P from agricultural and urban drainage. Thomas (1957) attempted to correlate nutrient inputs to the trophic state of several Swiss lakes. Recognizing the importance of P as a limiting nutrient, Hutchinson and Bowen (1950), among others, used radioactive tracers to investigate the P cycle in lakes.

The identification of P as the nutrient that drives the eutrophication process motivated a very large expenditure of financial resources in North America and Europe beginning in the mid-1960's (WHO 1981). In North America this period is marked by two monumental studies. First, long-term limnological studies on Lake Washington by Edmondson (1970, 1977) and associates have documented quantitative changes in lake chemistry and biology following sewage diversion. Second, research on artificially fertilized lakes in the Experimental Lakes Region, Ontario, has provided unparallelled insights into lake eutrophication processes (Schindler 1974, 1977; Schindler et al. 1980). These include the evolution of nutrient limitation, the role of sediments and the hypolimnion in P recycling, and the importance of atmospheric N_2 and CO_2 as limiting nutrients. Reports published by Middlebrooks et al. (1973) and EPA (1979, 1980) include important papers on eutrophication processes and lake restoration.

This period of research has also witnessed one of the most successful experiments in applied aquatic ecology — the development and application of P-loading models to predict lake response to P enrichment (Metz 1985). This approach, pioneered in its theoretical development and application by Vollenweider (1968, 1975), is based on the concept that phytoplankton biomass is correlated with external P loadings once appropriate adjustments are made for lake depth and water residence time. The Vollenweider models have not only provided the first truly quantitative means of managing lakes on a worldwide basis (Vollenweider and Kerekes 1981), but they have spawned other approaches to quantify the relationship between P concentrations and loadings (e.g. Dillon and Rigler 1974; Chapra 1977; Imboden and Gachter 1978).

Phosphorus–Plankton Dynamics

In addition to understanding how lakes respond to altered P loadings, a primary goal in aquatic science is to *predict* the spatial and temporal behavior of major biological and chemical components in natural systems. The crucial role of P has motivated numerous studies to understand how primary and secondary production in freshwater aquatic systems are controlled by limiting concentrations of this nutrient. Research efforts can be grouped into five major categories: P cycling in lakes; eutrophication processes and mathematical modeling; P measurement and chemical compartments; microbial growth and cellular metabolism; and theories and hypotheses concerning P–phytoplankton dynamics. Research papers are widely scattered in the scientific literature. Recent reviews by Nalewajko and Lean (1980) and Cembella et al. (1984) provide entry points into the recent literature.

A major research thrust in P–plankton dynamics has been to determine how variable P_i supply rates control the outcome of species competition under steady-state conditions. This effort is imbedded in the pioneering studies of Droop (1974) on

[1] GLERL Contribution No. 475.

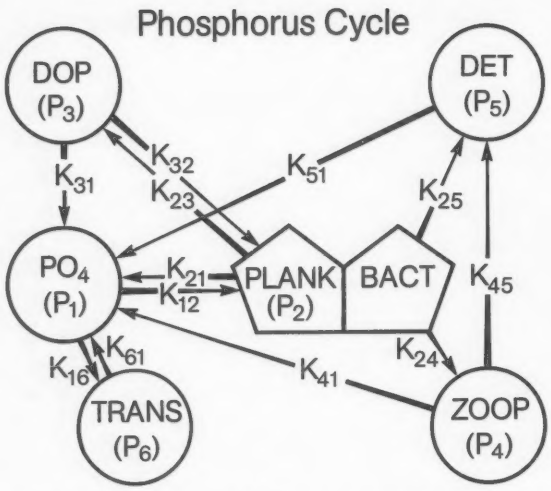


FIG. 1. Conceptual diagram of the P cycle in freshwater lakes (after Rigler 1973 and Golterman 1973). Compartments are orthophosphate (P_1), phytoplankton (P_2), dissolved organic P (P_3), zooplankton (P_4), detritus (P_5), and transport out of the epilimnetic zone (P_6). Bacteria are considered part of P_2. *K*'s are the rate constants for P movement among compartments.

experimentally based models for P-limited algal cell growth. Droop's cell quota model has motivated additional studies to develop refined models based on internal and external P pools (e.g. Rhee 1973, 1978), as well as generalized models integrating the enzyme-mediated kinetics of substrate transport, growth, and nutrient efflux (Button 1978). These models, which also include moderating effects of physical factors (Rhee and Gotham 1981; Tilman et al. 1982), form the theoretical basis for predicting the outcome of nutrient-based competition (e.g. Tilman and Kilham 1976; Rhee and Gotham 1980). Two significant advances in competition theory have recently been made. First, models based on species *resource* requirements have been developed (Tilman et al. 1982; Tilman 1982). Second, competition under nonsteady-state P_i supply rates, a condition that may better characterize P_i supplies in nature, is now being actively explored (e.g. Burmaster 1979; Sommer 1984).

A second thrust has been to develop bioassays to detect limiting nutrients in natural phytoplankton populations. This approach, initiated by Gerloff and Skoog (1954), Potash (1956), Thomas (1961), and Hughes and Lund (1962), is based primarily on growth-related physiological characteristics of P-limited algae. Detection of P limitation is usually based either on measurements of intracellular nutrient ratios (Redfield et al. 1963), surplus P or polyphosphate stores (Fitzgerald and Nelson 1966), cell-surface alkaline phosphatase activity (Kuenzler and Perras 1965), or the capacity of cells to take up limiting nutrients (Fitzgerald 1970).

Bioassay technology has been marked by two major advances. First, during the era of the C−P eutrophication controversy in the late 1960's (Vallentyne 1970; Likens 1972), Schindler (1971) demonstrated that conventional bioassays could yield false impressions of the nutrients causing accelerated lake eutrophication. Second, Healey (1979) demonstrated that short-term ^{14}C photosynthetic responses to P_i additions give misleading information. Phosphorus-limited cells temporarily suppress photosynthetic rates, diverting cellular energy to support rapid P_i uptake. State-of-the-art bioassay approaches are illustrated in Healey and Hendzel (1980) and Lean and Pick (1981).

Phosphorus Cycling

The intrinsic growth rates of microorganisms in P-limited systems are ultimately dependent on internal P recycling rates. Our understanding of the cycle in the early 1970's was reviewed by Rigler (1973) and Golterman (1973). A simplified compartment diagram, developed primarily from Rigler's (1973) article, shows the major components of the epilimnetic P cycle (Fig. 1). The model includes two primary biological compartments (phytoplankton and zooplankton) and three abiotic components (P_i, dissolved organic P (DOP), and detritus).

One of the earliest observations is that the P_i pool is exceedingly small and highly labile, with apparent turnover times on the order of minutes during summer in most natural environments (Pomeroy 1960; Rigler 1973). The kinetics of P movement in the epilimnion correspond best to a four-compartment model (Lean 1973). The dominant exchange is uptake and release of P_i by the particulate fraction, but some P is excreted by the microorganisms in the form of a low molecular weight compound (XP). Polycondensation of the low molecular weight compound produces a colloidal-size molecule and also releases P_i. Lean's model appears generalized, as similar results have been obtained for different lake types (e.g. Paerl and Downes 1978; Stainton 1980).

A principal impediment in modeling the P cycle is the difficulty of accurately measuring P_i and DOP concentrations. For example, P_i pool size cannot be determined by standard procedures because molybdenum blue methods grossly overestimate true P_i concentrations (Rigler 1973). The reason for the discrepancy between true P_i concentrations and colorimetric estimates (i.e. soluble reactive P) was attributed to P_i release by acid hydrolyses of organic compounds. Rigler's (1968) work spawned numerous efforts to measure P_i or bioavailable P (Chamberlain and Shapiro 1969; Peters 1978; Pettersson 1979; Nürnberg and Peters 1984). To date, however, the problem remains unresolved (Stainton 1980; Tarapchak 1983). Rigler's (1966) radiobioassay approach, which only estimates maximum possible P_i concentrations, is the acknowledged standard. Similarly, procedures for determining DOP concentrations and composition are often based on operational definitions or imperfect techniques (Strickland and Parsons 1972). Although some components of the DOP pool have been characterized, its precise chemical make up is unknown (Koenings and Hooper 1976; Francko and Heath 1979, 1982).

Problems in Phosphorus Cycling

The cumulative research effort on aquatic P cycling through the 1980's has raised additional, even more challenging problems than those envisioned in the early 1970's. Several crucial issues are summarized here.

Orthophosphate Uptake by Phytoplankton

The starting point for modeling P cycling is the P_i pool (Rigler 1973). However, the rate at which P_i enters the lower food web (through phytoplankton and possibly bacteria) cannot be quantified for two reasons. First, conventional radiotracer techniques measure gross, not net, P_i uptake (Lean and

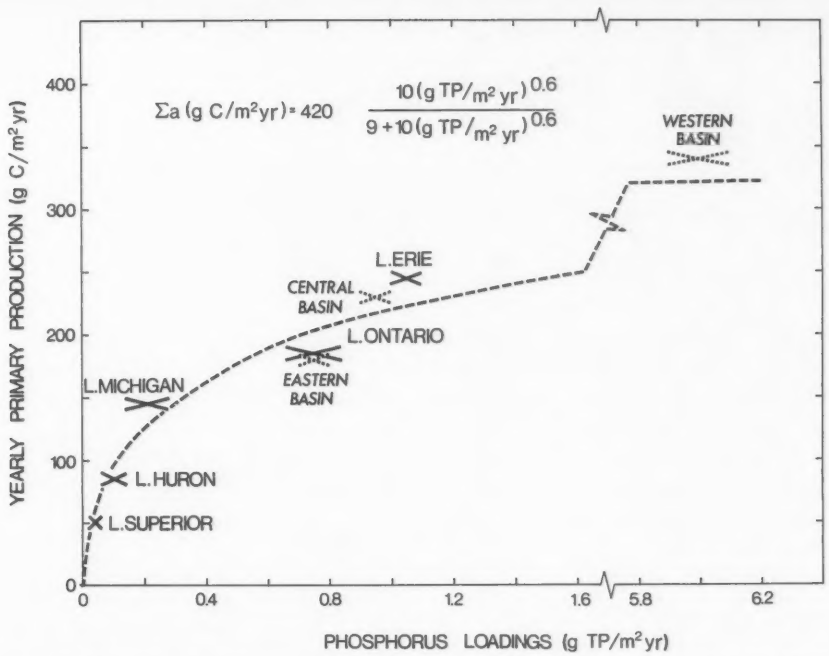


FIG. 2. Relationship between external P loadings and primary production in the Great Lakes (from Vollenweider et al. 1974).

Nalewajko 1976; Lehman 1984). Second, the size of the P_i pool, as pointed out, cannot be measured accurately. The need to resolve this problem has been sharply focused by the fact that phytoplankton appear to be growing at maximal rates, despite the presence of only *minute* concentrations of the limiting nutrient (Goldman et al. 1979; Currie 1984). This apparent paradox may be explained in one or both of two ways. Algae either have extremely high-affinity uptake systems (i.e. systems of natural populations are much more efficient than suggested by measurements on laboratory monocultures), or P may be obtained from sources other than bulk ambient P_i. Potential sources of nonbulk P include P_i from the DOP pool mediated by cell-surface alkaline phosphatase formation (Kuenzler 1965; Kuenzler and Perras 1965), or P_i from high-phosphate plumes generated by actively feeding zooplankton (Lehman and Scavia 1982). Rates of net P_i uptake by phytoplankton from the bulk P_i pool and the relative importance of other P sources must be quantified if significant advances are to be made in understanding how P_i functions as a limiting nutrient.

Bacterial Phosphorus Sources

Recent studies on P utilization by heterotrophic bacteria and their production rates suggest that the assumed role of these organisms as primary consumers of DOP may have to be radically redefined. Bacterial production rates in some systems can rival phytoplankton production rates (Pedros-Alio and Brock 1972). Several reports since Rigler's (1956) pioneering study suggest that bacteria may not only use P_i but may, in fact, outcompete phytoplankton at ambient P_i levels (e.g. Paerl and Lean 1976; Currie and Kalff 1984). Hence, if bacteria use primarily P_i, their assumed role as mineralizers of the DOP pool (which is thought to provide P_i for algae) must also be critically evaluated.

Zooplankton Phosphorus Recycle

The role of herbivorous zooplankton (P_2) in regenerating inorganic nutrients was recognized ever since Gardiner's (1937) early experiments on nutrient release from marine plankton. However, the contribution made by zooplankton to the total P budget is usually impossible to calculate because hydrological budgets and fluvial fluxes for most lakes are unknown. Recent work, however, shows that epilimnetic zooplankton P_i recycling in the large lakes may be a primary regenerative mechanism. Based on nutrient budgets and in situ grazing measurements, zooplankton in Lake Washington supply 10 times more P_i to the surface layer during summer than enters the lake from all sources (Lehman 1980). Such results argue for additional studies on zooplankton P_i regeneration in relation to in situ phytoplankton demand. It also is generally assumed that P_i is the primary form of P released by zooplankton (Rigler 1973). However, this assumption must be validated because DOP compounds can test as P_i when measured by conventional methods (e.g. Stainton 1980).

Dissolved Organic Phosphorus

The DOP pool (P_3) occupies a key position in P cycling because algae, zooplankton, and bacteria contribute to it. The pool is thought to be composed of numerous compounds, ranging from low molecular weight, highly labile compounds to large, biologically refractory compounds (Chamberlain 1968; Hooper 1973). However, the chemical composition of the pool and recycling rates of individual compounds are poorly understood. The major compounds and their fluxes, including recycling mechanisms for biologically refractory compounds, must be better known if the close coupling between nutrient-dependent bacteria–phytoplankton dynamics is to be better

TABLE 1. Selected studies on eutrophication in the Great Lakes.

Contribution	Reference(s)
EUTROPHICATION PROCESSES AND MODELS	
P loading, models, and budgets	
Classical P loading Lake–response relationships	Vollenweider et al. 1974, 1980
P budgets and eutrophication and water quality models	Snodgrass and O'Melia 1975; Chapra 1977, 1980; Canale and Squire 1976; Chapra and Robertson 1977; Schelske 1979; Reckhow 1979; Snodgrass 1979; Chapra and Sonzogni 1979; Di Toro and Matystik 1979; Fraser 1980; Chapra and Dobson 1981; Janus and Vollenweider 1981; Dolan et al. 1981
Atmospheric P loading	
Quantitative importance of atmospheric P loadings	Kilham and Titman 1975; Murphy and Doskey 1976; Eisenreich et al. 1977; Parker et al. 1981
Ecosystem modeling	
P-Phytoplankton dynamics	Thomann et al. 1977; Scavia and Chapra 1977; Scavia 1979; 1980; Thomann and Segna 1980; Di Toro 1980; Bierman and Dolan 1982
P CYCLING	
Dissolved P composition	
SRP measurements and chemical composition	Tarapchak and Rubitschun 1981; Tarapchak et al. 1981; Tarapchak et al. 1982a, 1982b, 1982c; Tarapchak 1983
Short-term P cycling	
P cycling in the Bay of Quinte	Lean and Charlton 1976
P CYCLING AND REGENERATION	
Epilimnion	
Mass-balance calculations	Stadelmann et al. 1974; Stadelmann and Fraser 1974; McCormick and Tarapchak 1984
Sediments	
Role of sediments in P regeneration	Gumerman 1970; Mortimer 1971; Bannerman et al. 1974; Freedman and Canale 1977
Zooplankton	
P recycling by zooplankton	Ferrante 1976; Kordstad 1983
Bacterial	
Bacterial degradation of zooplankton fecal pellets	Ferrante and Ptak 1978
Benthic invertebrates	
P recycling by benthic invertebrates	Gardner et al. 1981; Nalepa et al. 1983
Bioavailable P	
Bioavailable P in sediments and particulate materials entering the Great Lakes	Cowen and Lee 1976; DePinto et al. 1981; Logan et al. 1979; Williams et al. 1976a, 1976b; Williams et al. 1980; Dorich et al. 1980; Sonzogni et al. 1982; Young and DePinto 1982; Young et al. 1982
P–PLANKTON DYNAMICS	
Bioassays for P limitation	
Detection of P and Si limitation	Schelske et al. 1974; Schelske 1975, 1984; Lean and Nalewajko 1979; Lean et al. 1983
Cladophora growth	
Ecological studies and modeling of *Cladophora*	Rosemarin 1982; Auer and Canale 1982a, 1982b; Canale and Auer 1982

understood (Wetzel 1983).

Alkaline Phosphatase

The importance of P_i regeneration by alkaline phosphatase, other dissolved enzymes, and physical–chemical processes is critically in need of investigation, particularly in large lakes where most of the P_i supply during summer is recycled within the epilimnion (Wetzel 1983). Intensive research over the last 10 yr has identified three distinct regenerative mechanisms: release of P_i from colloids (Lean 1973); hydrolysis of dissolved low molecular weight organic P compounds by cell-surface alkaline phosphatase or other dissolved enzymes (Berman 1970; Wetzel 1981; Stewart and Wetzel 1982); and photochemical P_i release from ferric iron-dissolved humic materials (Koenings and Hooper 1976; Francko and Heath 1983). The overall importance of these mechanisms, relative to zooplankton P_i regeneration, must be quantified in different lake types.

Detritus

The role of detritus (P_5) is epilimnetic P cycling has largely been ignored. Detritus, produced primarily by zooplankton grazing and by cell death, is a potentially important component. These materials serve as a temporary P sink, provide substrate for bacteria, and may remove relatively large quantities of P from the epilimnion by sinking into the hypolimnion.

The Deteriorated Great Lakes Resource

The Great Lakes system, containing over one fifth of the world's fresh surface water, represents an immensely valuable North American resource (Ragotzkie 1974; Sonzogni et al. 1983). The multipurpose use of this system can be dramatically illustrated as follows.

Commercial fisheries and sports fishery total $160 million and over $1 billion per year, respectively, with about 2 million people participating. Water withdrawals, supplying drinking water for nearly 25 million people, total 45 billion gallons per

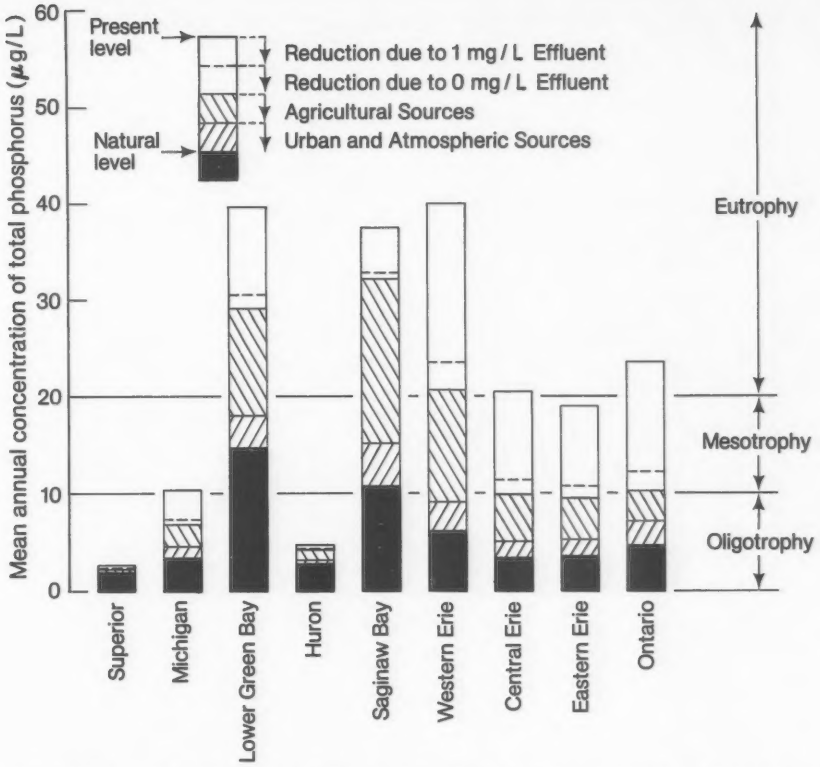


FIG. 3. Results of a budget model showing the effects of a 1 mg/L restriction on point-source discharges of total P into the Great Lakes system (from Chapra and Robertson 1977).

day. Great Lakes shipping, dominated by bulk cargoes of iron ore, coal, grain, and limestone, total over 200 million tons per year. Waste disposal from municipal and industrial plants totals over 20 billion gallons per day. Water from the lakes is also used as coolant in nuclear and fossil fuel power generation in the multibillion dollar energy industry. Recreation, sports fishing, and tourism in the Great Lakes basin are $1 billion per year industry (E. Aubert, Great Lakes Environmental Research Laboratory, Ann Arbor, MI, and C. Herdendorf, Ohio State University, Columbus, OH, pers. comm.).

Gradual increases in P loadings over the last 100 yr resulting from human population increases have produced recognizable symptoms of deteriorating water quality that are especially severe in the lower Great Lakes (Beeton 1965). For example, the lower portions of Green Bay, Saginaw Bay, and the western basin of Lake Erie showed severe signs of hypereutrophication by the early 1960's (Burns and Ross 1972; Tarapchak and Stoermer 1976). This problem, recognized by the governments of the United States and Canada, culminated in the Great Lakes Water Quality Agreements of 1972 and 1978. The objectives of the first plan were to restore year-round aerobic conditions in the bottom waters of Lake Erie's central basin, reduce algal growth in Lakes Erie and Ontario, and stabilize Lake Superior and Lake Huron as oligotrophic lakes (IJC 1974). The second agreement was expanded to reduce P inputs from diffuse sources, reduce P in household detergents (to 0.5% by weight) where necessary to meet specified loading allocations, and maintain an active research program in P control (IJC 1978). Large-scale P loading controls in the 1970's, based on reformulating detergents to reduce their P content (especially in Canada) and improving sewage treatment facilities, have resulted in recent water quality improvements in Lakes Ontario and Erie (Dobson 1981).

Great Lakes Research Focus

Phosphorus research in the Great Lakes system has had a strong practical orientation with two primary thrusts: monitoring and water quality surveillance by the Environmental Protection Agency and Environment Canada, and the use of mathematical models to determine present and future trophic conditions in the lakes. The first effort to quantify the relationship between P loadings and lake response was that of Vollenweider et al. (1974) (Fig. 2). These and subsequent analyses (Table 1, P loading, models, and budgets) clearly demonstrate the prestine nature of Lake Superior relative to the severe nutrient overloading of western Lake Erie. Reports dealing with water quality, the overenrichment problem, and proposed remedial actions are contained in numerous IJC reports. Those cited in Table 2 serve as a point of entry to IJC literature.

The use of mathematical models to study plankton dynamics and eutrophication processes occupies a central theme in Great Lakes research (Loehr et al. 1980). Three types of models have been applied. The first centers around the P loading concept. These models, based on mass balances of P inflow, outflow,

TABLE 2. Selected IJC reports on P dynamics and eutrophication (reports available from the International Joint Commission, Great Lakes Regional Office Library, 100 Ouellette Avenue, Windsor, Ont. N9A 6T3).

Report	Publication date
GENERAL	
1972 and 1978 Great Lakes water quality agreements: a bibliography — November 1983	1983
PLUARG AND BIOAVAILABILITY	
Availability of phosphorus in different sources entering the Great Lakes for Algal Growth	1979
Contribution of phosphorus from agricultural land to streams by surface runoff	1978
Biological availability of phosphorus	1978
Nonpoint source pollution abatement in the Great Lakes basin: an overview of post-PLUARG developments	1983
P LOADING AND MANAGEMENT STRATEGIES	
Phosphorus load reduction supplement to Annex 3 of the 1978 agreement between the United States of America and Canada on Great Lakes water quality	1983
1981 municipal and industrial phosphorus loadings to the Great Lakes	1982
Report on differences in the Great Lakes phosphorus load estimates	1979
Relative costs of achieving various levels of phosphorus control at municipal wastewater treatment plants in the Great Lakes basin	1978
Environmental management strategy for the Great Lakes system	1982
1981 municipal and industrial phosphorus loadings to the great lakes	1982
Supplement report on phosphorus management strategies	1981
Phosphorus management for the Great Lakes: final report of the Phosphorus Management Strategies Task Force	1980
GREAT LAKES WATER QUALITY	
1983 report on Great Lakes water quality, appendix, Great Lakes surveillance 1983	1983

and sedimentation, are designed to assess trophic state as a function of past, present, and future loading rates (e.g. Chapra 1977). They ignore the effects of internal dynamics. The second class, often termed "eutrophication models," are designed to simulate and predict phytoplankton biomass dynamics (e.g. Thomann et al. 1977). These models normally predict biomass as a function of first-order processes such as phytoplankton production, respiration, sinking, and nutrient cycling. The third class, complex ecosystem models, are designed to synthesize information on physical, chemical, and biologic processes and to analyze controls of system structure and function. These models have provided important insight into physical and chemical controls of plankton dynamics and nutrient regeneration processes in the Great Lakes (e.g.Scavia 1979).

The use of P budget models to predict potential improvements in Great Lakes water quality resulting from P reductions has attracted immense interest. The IJC recommended that all point-source P discharges in the Great Lakes system be limited to 1 mg/L (IJC 1976). Chapra's (1977) model illustrates the predictive capabilities of budget models (Fig. 3). His model, based on forcing functions such as population and land use (including wastes from domestic sources, land runoff, and the atmosphere), showed that the 1 mg/L effluent restriction would generally improve water quality over much of the Great Lakes. Only minor improvements would be observed in Lake Superior and Lake Huron, Lake Michigan would return to its original oligotrophic state, and total P levels in central and eastern Lake Erie and Lake Ontario would decrease by about one half. However, the 1 mg/L restriction would not result in major improvements in water quality in western Lake Erie, Green Bay, or Saginaw Bay because of high natural loadings in these areas.

Great Lakes Research Needs

The use of eutrophication and complex ecosystem models has clearly identified our incomplete understanding of P–plankton dynamics and P cycling in the Great Lakes system. Great Lakes research on P dynamics has focused largely on assessing eutrophication and predicting how changes in nutrient loadings will affect water quality (Table 1, Eutrophication Processes and Models). Unfortunately, basic research on P-related biological and chemical processes needed to refine the predictive capabilities of mathematical models has lagged behind applied research efforts. For example, the only intensive long-term investigation into phytoplankton nutrient limitation and its effects on primary production and phytoplankton seasonal succession on the American side is that of Schelske and associates (Schelske and Stoermer 1971, 1972; Schelske 1975, 1979, 1984; Schelske et al. 1974). These collected works have demonstrated the role of P and Si limitation in the Great Lakes eutrophication process, and have also motivated studies to reconstruct the history of cultural eutrophication in the Great Lakes using nutrients and microfossils in lake sediments (Harris and Vollenweider 1982; Schelske et al. 1983).

Efforts to correct the overenrichment problem in the Great Lakes motivated the formation of the Pollution from Land Use Activities Reference Group (PLUARG). This group, formed in 1972 under the auspices of the International Joint Commission, was established to carry out the reference contained in the Water Quality Agreement of 1972, and was instrumental in refinement of management strategies based on P loading and budget models. PLUARG has had a major impact on the direction of P-related eutrophication research by focusing attention on the need for intensive studies on P bioavailability of particulate materials entering the lakes. This work has provided important information on the availability of different chemical forms of extractable P (e.g. Cowen and Lee 1976; Williams et al. 1980). A comprehensive review of extraction schemes and the bioavailability of different chemical fractions has been presented by Sonzogni et al. (1982).

Basic research in the Great Lakes has provided only first-order insights into primary and secondary production controls. For example, internal recycling apparently supplies most of the P_i required for algal growth during summer (Stadelmann and Fraser 1974). However, many questions regarding the subtle, but crucial role of P cycling remain unanswered. What are the relative regenerative contributions of zooplankton, enzyme activity, and colloidal displacement, respectively, to the total P_i demand of the phytoplankton? How much of the required P_i

diffuses from the nutrient-rich hypolimnion in Lakes Erie and Ontario into surface waters during summer? What fraction of this requirement is supplied by sediment resuspension at spring overturn? Do bacteria compete with algae for the same P source, and do algae obtain significant P_i from organic compounds? What is the chemical composition of the DOP pool, and how is this material recycled if bacteria are using P_i? Obviously, answers to these questions are necessary if P cycling in the Great Lakes is to be understood.

The P–Plankton Dynamics Symposium, consisting of 31 invited scientists from North America and Europe, was held at the 27th Conference on Great Lakes Research (International Association of Great Lakes Research), Brock University, St. Catharines, Ont. The following 13 papers, including two invited manuscripts, form part of the Symposium proceedings. Other manuscripts will be published later. This issue is available from Supply and Services Canada, Ottawa, Ont. The complete Symposium proceedings will be published in late 1986 as a special summary report by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI.

Acknowledgements

We thank the Organizing Committee of the 27th Conference on Great Lakes Research, particularly Dr. Michael Dickman for the invitation to convene this Symposium and for his assistance in arranging the program. Ms. Vicki Lowenberger graciously arranged accommodations, and Brock University provided excellent facilities. Dr. Richard Vollenweider and Dr. Jack Vallentyne provided information on Great Lakes eutrophication, and John Gannon provided IJC reports. Partial travel support and publication costs for American participants were provided by the Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, MI. Norma Lojewski and George H. Townsend typed the manuscript.

References

AUER, M. T., AND R. P. CANALE. 1982a. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. J. Great Lakes Res. 8: 84–92.

1982b. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. J. Great Lakes Res. 8: 93–99.

BANNERMAN, R. T., D. E. ARMSTRONG, G. C. HOLDREN, AND R. F. HARRIS. 1974. Phosphorus mobility in Lake Ontario sediments, p. 158–178. *In* Proc. 17th Conf. Great Lakes Res., International Association for Great Lakes Research, Toronto, Ont.

BEETON, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

BIERMAN, V. J., AND D. M. DOLAN. 1982. Modeling phytoplankton–nutrient dynamics in Saginaw Bay, Lake Huron. J. Great Lakes Res. 7: 409–439.

BRUMASTER, D. E. 1979. The unsteady continuous culture of phosphate-limited *Monochrysis lutherei* Droop: experimental and theoretical analyses. J. Exp. Mar. Biol. Ecol. 39: 167–186.

BURNS, N. M., AND C. ROSS. 1972. Project Hypo. Canada Centre for Inland Waters, Paper No. 6, and the United States Environmental Protection Agency, Technical Report TS-05-71-208-24.

BUTTON, D. K. 1978. On the theory of nutrient control of microbial growth kinetics. Deep-Sea Res. 25: 1163–1177.

CANALE, R. P., AND M. T. AUER. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res. 8: 112–125.

CANALE, R. P., AND J. SQUIRE. 1976. A model for total phosphorus in Saginaw Bay. J. Great Lakes Res. 2: 364–373.

CEMBELLA, A. D., N. J. ANTIA, AND P. J. HARRISON. 1984. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective: Part I. CRC Crit. Rev. Microbiol. 10: 317–391.

CHAMBERLAIN, W. M. 1968. A preliminary investigation of the nature and importance of soluble organic phosphorus in the phosphorus cycle of lakes. Ph.D. thesis, University of Toronto, Toronto, Ont. 232 p.

CHAMBERLAIN, W. M., AND J. SHAPIRO. 1969. On the biological significance of phosphate analysis: comparison of standard and new methods with a bioassay. Limnol. Oceanogr. 14: 921–927.

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Environ. Eng. Div. Am. Soc. Civ. Eng. 103: 147–161.

1980. Simulation of recent and projected total phosphorus trends in Lake Ontario. J. Great Lakes Res. 6: 101–112.

CHAPRA, S. C., AND H. F. H. DOBSON. 1981. Quantification of the lake trophic typologies of Naumann (surface quality) and Thienemann (oxygen) with special reference to the Great Lakes. J. Great Lakes Res. 7: 182–193.

CHAPRA, S. C., AND A. ROBERTSON. 1977. Great Lakes eutrophication: the effects of point source control of total phosphorus. Science (Wash., DC) 196: 1448–1450.

CHAPRA, S. C., AND W. C. SONZOGNI. 1979. Great Lakes total phosphorus budget for the mid 1970's. J. Water Pollut. Control Fed. 51: 2524–2533.

COWEN, W. F., AND G. F. LEE. 1976. Phosphorus availability in particulate materials transported by urban runoff. J. Water Pollut. Control Fed. 48: 580–591.

CURRIE, D. J. 1984. Phytoplankton growth and the microscale nutrient patch hypothesis. J. Plankton Res. 6: 591–599.

CURRIE, D. J., AND J. KALFF. 1984. The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in freshwater. Limnol. Oceanogr. 29: 311–321.

DEPINTO, J. V., T. C. YOUNG, AND S. C. MARTIN. 1981. Algal-available phosphorus in suspended sediments from lower Great Lakes tributaries. J. Great Lakes Res. 7: 311–325.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

DI TORO, D. M. 1980. The effect of phosphorus loading on dissolved oxygen in Lake Erie, p. 191–205. *In* R. C. Loehr, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

DI TORO, D. M., AND W. F. MATYSTIK, JR. 1979. Phosphorus recycle and chlorophyll in the Great Lakes. J. Great Lakes Res. 5: 233–245.

DOBSON, H. F. H. 1981. Trophic conditions and trends in the Laurentian Great Lakes. W.H.O. Water Qual. Bull. 6: 146–151.

DOLAN, D. M., A. K. YVI, AND R. D. GEIST. 1981. Evaluation of river load estimation methods for total phosphorus. J. Great Lakes Res. 7: 207–214.

DORICH, R. A., D. W. NELSON, AND L. E. SOMMERS. 1980. Algal availability of sediment phosphorus in drainage water of the Black Creek Watershed. J. Environ. Qual. 9: 557–563.

DROOP, M. R. 1974. The nutrient status of algal cells in continuous culture. J. Mar. Biol. Assoc. U.K. 54: 825–855.

EDMONDSON, W. T. 1970. Phosphorus, nitrogen and algae in Lake Washington after diversion of sewage. Science (Wash., DC) 169: 690–691.

1977. Recovery of Lake Washington from eutrophication, p. 102–109. *In* J. Cairns, Jr., K. L. Dickson, and E. E. Herricks. [ed.] Recovery and restoration of damaged ecosystems, University Press of Virginia, Charlottesville, VA.

EINSELE, W. 1941. Die Umsetzung von Zugefuhrtem, anorganischen Phosphat im eutrophen See und ihre Ruckwirkung auf seinen Gesamthaushalt. Z. Fisch. 39: 408–438.

EISENREICH, S. J., P. J. EMMLING, AND A. M. BEETON. 1977. Atmospheric loading of phosphorus and other chemicals to Lake Michigan. J. Great Lakes Res. 3: 291–304.

LEAN, D. R. S., AND M. CHARLTON. 1976. A study of phosphorus kinetics in a lake ecosystem, p. 283–294. *In* J. O. Nriagu [ed.] Environmental biogeochemistry. Vol. 1: Carbon, nitrogen, phosphorus, sulfur, and selenium cycles. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

LEAN, D. R. S., AND C. NALEWAJKO. 1976. Phosphate exchange and organic phosphorus excretion by freshwater algae. J. Fish. Res. Board Can. 33: 1312–1323.

1979. Phosphorus turnover time and phosphorus demand in large and small lakes. Arch. Hydrobiol. Beih. 13: 120–132.

LEAN, D. R. S., AND F. R. PICK. 1981. Photosynthetic response of lake plankton to nutrient enrichment: test for nutrient limitation. Limnol. Oceanogr. 26: 1001–1019.

LEHMAN, J. T. 1980. Release and cycling of nutrients between planktonic algae and herbivores. Limnol. Oceanogr. 25: 620–632.

1984. Grazing, nutrient release, and their impacts on the structure of phytoplankton communties, p. 40–72. *In* D. G. Meyers and J. R. Strickler [ed.] Trophic interactions within aquatic ecology. American Association for Advancement of Science Selected Symposium No. 85.

LEHMAN, J. T., AND D. SCAVIA. 1982. Microscale patchiness of nutrients in plankton communities. Science (Wash., DC) 216: 729–730.

LIKENS, G. E. [ED.] 1972. Nutrients and eutrophication: the limiting-nutrient controversy. Special Symposia Vol. 1. American Society of Limnology and Oceanography, Grafton, WI. 328 p.

LOEHR, R. C., C. S. MARTIN, AND W. RAST [ED.] 1980. Phosphorus management strategies for lakes. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

LOGAN, T. J., T. O. OLOYA, AND S. YAKSICH. 1979. Phosphate characteristics and bioavailability of suspended sediments from streams draining into Lake Erie. J. Great Lakes Res. 5: 112–123.

MCCORMICK, M. J., AND S. J. TARAPCHAK. 1984. Uncertainty analysis of calculated nutrient regeneration rates in Lake Michigan. Can. J. Fish. Aquat. Sci. 41: 206–211.

METZ, W. 1985. The lake doctor. Sat. Night 100: 13–17.

MIDDLEBROOKS, E. J., D. H. FALKENBORG, AND T. MALONEY [ED.] 1973. Modeling the eutrophication process, p. 228. Proceedings of a Workshop held at Utah State University, Logan, Utah. Report PRWG 136-1, Utah Water Research Laboratory and Division of Environmental Engineering.

MORTIMER, C. H. 1971. Chemical exchanges between sediments and water in the Great Lakes — speculations on probable regulatory mechanisms. Limnol. Oceanogr. 16: 387–404.

MURPHY, T. J., AND P. V. DOSKEY. 1976. Inputs of phosphorus from precipitation to Lake Michigan. J. Great Lakes Res. 2: 60–70.

NALEPA, T. F., W. S. GARDNER, AND J. M. MALCZYK. 1983. Phosphorus release by three kinds of benthic invertebrates: effects of substrate and water medium. Can. J. Fish. Aquat. Sci. 40: 810–813.

NALEWAJKO, C., AND D. R. S. LEAN. 1980. Phosphorus, p. 235–258. *In* I. Morris [ed.] The physiological ecology of phytoplankton. University of California Press, Berkeley, CA.

NATIONAL ACADEMY OF SCIENCES (NAS). 1969. Eutrophication: causes, consequences, correctives. Proceedings of a Symposium. National Academy of Sciences,Washington, DC.

NÜRNBERG, G. K., AND R. H. PETERS. 1984. Biological availability of soluble reactive phosphours in anoxic and oxic freshwaters. Can. J. Fish. Aquat. Sci. 41: 757–765.

PAERL, H. W., AND M. T. DOWNES. 1978. Biological availability of low versus high molecular weight reactive phosphorus. J. Fish. Res. Board Can. 35: 1639–1643.

PAERL, H., AND D. R. S. LEAN. 1976. Visual observations of phosphorus movement between algae, bacteria, and abiotic particles in lake waters. J. Fish. Res. Board Can. 33: 2805–2813.

PARKER, J. I., G. T. TISUE, C. W. KENNEDY, AND C. A. SEILS. 1981. Effects of atmospheric precipitation additions on phytoplankton photosynthesis in Lake Michigan water samples. J. Great Lakes Res. 7: 21–28.

PEDROS-ALIO, C., AND T. D. BROCK. 1982. Assessing biomass and production of bacteria in eutrophic Lake Mendota, Wisconsin. Appl. Environ. Microbiol. 44: 203–218.

PETERS, R. H. 1978. Concentrations and kinetics of phosphorus fractions in water from streams entering Lake Memphremagog. J. Fish. Res. Board Can. 35: 315–328.

PETTERSSON, K. 1979. Enzymatic determination of orthophosphate in natural waters. Int. Rev. Gesamten Hydrobiol. 64: 585–607.

POMEROY, L. R. 1960. Residence time of dissolved phosphate in natural waters. Science (Wash., DC) 131: 1731–1732.

POTASH, M. 1956. A biological test for determining the potential productivity of water. Ecology 37: 631–639.

RAGOTZKIE, R. A. 1974. The Great Lakes rediscovered. Am. Sci. 62: 454–464.

RECKHOW, K. H. 1979. Empirical lake models for phosphorus: development, applications, limitations and uncertainty, p. 193–221. *In* D. Scavia and R. Robertson [ed.] Perspectives on lake ecosystem modeling. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

REDFIELD, A. C., B. H. KETCHUM, AND F. A. RICHARDS. 1963. The influence of organisms on the composition of sea-water, p. 26–77. *In* The sea. Vol. 2. Wiley Interscience, New York, NY.

RHEE, G-Y. 1973. A continuous culture study of phosphate uptake, growth rate and polyphosphate in *Scenedesmus* sp. J. Phycol. 9: 495–506.

1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnol. Oceanogr. 23: 10–25.

RHEE, G-Y., AND I. J. GOTHAM. 1980. Optimum N:P ratios and coexistence of planktonic algae. J. Phycol. 16: 486–489.

1981. The effect of environmental factors on phytoplankton growth: temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26: 635–648.

RIGLER, F. H. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37: 550–562.

1966. Radiobiological analysis of inorganic phosphorus in lake water. Verh. Int. Ver. Limnol. 16: 465–470.

1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures orthophosphate in lake water. Limnol. Oceanogr. 13: 7–13.

1973. A dynamic view of the phosphorus cycle in lakes, p. 539–572. *In* E. J. Griffith, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] Environmental phosphorus handbook. John Wiley & Sons, New York, NY.

ROSEMARIN, A. S. 1982. Phosphorus nutrition of two potentially competing filamentous algae, *Cladophora glomerata* (L.) Kutz and *Stigeclonum glomerata* (L.) Kutz and *Stigeclonum tenue* (Agardh) Kutz from Lake Ontario. J. Great Lakes Res. 8: 66–72.

SAWYER, C. N. 1947. Fertilization of lakes of agricultural and urban drainage. N. Engl. Water Works Assoc. 61: 109–127.

SCAVIA, D. 1979. Examination of phosphorus cycling and control of phytoplankton dynamics in Lake Ontario with an ecological model. J. Fish. Res. Board Can. 36: 1336–1346.

1980. An ecological model of Lake Ontario. Ecol. Model. 8: 49–78.

SCAVIA, D., AND S. C. CHAPRA. 1977. Comparison of an ecological model of Lake Ontario and phosphorus loading models. J. Fish. Res. Board Can. 34: 286–290.

SCHELSKE, C. L. 1975. Silica and nitrate depletion as related to rate of eutrophication in Lake Michigan, Lake Huron, and Lake Superior, p. 277–298. *In* A. D. Hasler [ed.] Coupling of land and water systems. Springer, New York, NY.

1979. The role of phosphorus in Great Lakes eutrophication: is there a controversy? J. Fish. Res. Board Can. 36: 286–288.

1984. *In situ* and natural phytoplankton assemblage bioassays, p. 15–47. *In* L. E. Shubert [ed.] Algae as ecological indicators. Academic Press, Inc. Limited, London.

SCHELSKE, C. L., E. D. ROTHERMAN, E. F. STOERMER, AND M. A. SANTIAGO. 1974. Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. Limnol. Oceanogr. 19: 409–419.

SCHELSKE, C. L., AND E. F. STOERMER. 1971. Eutrophication, silica depletion, and predicted changes in algal quality in Lake Michigan. Science (Wash., DC) 173: 423–424.

1972. Phosphorus, silica, and eutrophication in Lake Michigan, p. 157–171. *In* G. E. Likens [ed.] Nutrients and eutrophication: the limiting-nutrient controversy. Special Symposia Vol. 1. American Society of Limnology and Oceanography, Grafton, WI. 328 p.

SCHELSKE, C. L., E. F. STOERMER, D. J. CONLEY, J. A. ROBBINS, AND R. M. GLOVER. 1983. Early eutrophication in the lower Great Lakes: new evidence from biogenic silica in sediments. Science (Wash., DC) 222: 320–322.

SCHINDLER, D. W. 1971. Carbon, nitrogen, and phosphorus and the eutrophication of freshwater lakes. J. Phycol. 7: 321–329.

1974. Eutrophication and recovery in experimental lakes: implications for lake management. Science (Wash., DC) 184: 897–898.

1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

SCHINDLER, D. W., T. RUSZCZYNSKI, AND E. J. FEE. 1980. Hypolimnion injection of nutrient effluents as a method for reducing eutrophication. Can. J. Fish. Aquat. Sci. 37: 320–327.

SNODGRASS, W. J. 1979. Predictive water quality models for the Great Lakes, p. 171–191. *In* D. Scavia and R. Robertson [ed.] Perspectives on lake ecosystem modeling. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

SNODGRASS, W. J., AND C. R. O'MELIA. 1975. Predictive model for phosphorus in lakes. Environ. Sci. Technol. 9: 937–944.

SOMMER, U. 1984. The paradox of the plankton: fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnol. Oceanogr. 29: 633–636.

SONZOGNI, W. C., S. C. CHAPRA, D. E. ARMSTRONG, AND T. J. LOGAN. 1982. Bioavailability of phosphorus inputs to lakes. J. Environ. Qual. 11: 555–563.

SONZOGNI, W. C., A. ROBERTSON, AND A. M. BEETON. 1983. Great Lakes management: ecological factors. Environ. Manage. 7: 531–542.

STADELMANN, P., AND A. FRASER. 1974. Phosphorus and nitrogen cycle on a transect in Lake Ontario during the International Field Year 1971–1973. (IFYGL), p. 92–107. Proc. 17th Conf. Great Lakes Res., International Association for Great Lakes Research, Toronto, Ont.

STADELMANN, P., J. E. MOORSE, AND E. PICKETT. 1974. Primary production in relation to temperature structure, biomass concentration, and light conditions at an inshore and offshore station in Lake Ontario. J. Fish. Res.

Board Can. 31: 1215–1232.

STAINTON, M. P. 1980. Errors in molybdenum blue methods for determining orthophosphate in freshwater. Can. J. Fish. Aquat. Sci. 37: 472–478.

STEWART, A. J., AND R. G. WETZEL. 1982. Phytoplankton contribution to alkaline phosphatase activity. Arch. Hydrobiol. 93: 265–271.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167 (2nd ed.): 310 p.

TARAPCHAK, S. J. 1983. Soluble reactive phosphorus measurements in lake water: evidence for molybdate enhanced hydrolysis. J. Environ. Qual. 12: 105–108.

TARAPCHAK, S. J., S. M. BIGELOW, AND C. RUBITSCHUN. 1982a. Overestimation of orthophosphorus concentrations in surface waters of southern Lake Michigan: effects of acid and ammonium molybdate. Can. J. Fish Aquat. Sci. 39: 296–304.

1982b. Soluble reactive phosphorus measurements in Lake Michigan: filtration artifacts. J. Great Lakes Res. 8: 550–557.

TARAPCHAK, S. J., R. L. CHAMBERS, AND S. M. BIGELOW. 1982c. Soluble reactive phosphorus measurements in Lake Michigan: causes of method-specific differences. J. Great Lakes Res. 8: 700–710.

TARAPCHAK, S. J., AND C. RUBITSCHUN. 1981. Comparison of soluble reactive phosphorus and orthophosphorus concentrations at an offshore station in southern Lake Michigan. J. Great Lakes Res. 7: 290–298.

TARAPCHAK, S. J., D. R. SLAVENS, AND L. M. MALONEY. 1981. Abiotic versus biotic uptake of radiophosphorus in lake water. Can. J. Fish. Aquat. Sci. 38: 889–895.

TARAPCHAK, S. J., AND E. F. STOERMER. 1976. Environmental status of Lake Michigan. Vol. 4. Phytoplankton. Argonne National Laboratory, Report ANL-40. Argonne National Laboratory, Argonne, IL.

THOMANN, R. V., AND J. S. SEGNA. 1980. Dynamic phytoplankton–phosphorus model of Lake Ontario: ten-year verification and simulations, p. 153–190. *In* R. C. Loehr, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

THOMANN, R. V., R. P. WINFIELD, AND D. S. SZUMSKI. 1977. Estimated responses of Lake Ontario phytoplankton biomass to varying nutrient levels. J. Great Lakes Res. 3: 123–131.

THOMAS, E. A. 1957. Der Zurichsee, sein Wasser and sein Boden. Jahrb. Zurichsee. 17: 173–208.

1961. Vergleiche Uber die Planktonproduktion in Flaschen und im Plankton-Test-Lot. Verh. Int. Ver. Limnol. 14: 140–146.

1973. Phosphorus and eutrophication, p. 585–611. *In* E. J. Griffith, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] Environmental phosphorus handbook. John Wiley & Sons, New York, NY.

TILMAN, D. 1982. Resource competition and community structure. Monographs in population biology, Vol. 17. Princton University Press, Princton, NJ.

TILMAN, D., AND S. S. KILHAM. 1976. Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semicontinuous culture. J. Phycol. 12: 375–383.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372.

VALLENTYNE, J. R. 1970. Phosphorus and the control of eutrophication. Can. Res. Dev. May–June: 36–49.

1974. The algal bowl: lakes and man. Misc. Spec. Publ. 22. Environment Canada. 185 p.

VOLLENWEIDER, R. A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Technical Report DAS/CSI/68.27. Organization of Economic Cooperative Development, Paris, France. 182 p.

1975. Input–output models with special reference to the phosphorus loading concept in limnology. Schweiz. Hydrol. 37: 53–84.

VOLLENWEIDER, R. A., AND J. KEREKES. 1981. OECD cooperative program on monitoring of inland waters (eutrophication control). Syntheses Report. OECD Secretariat, Environmental Directorate, Paris, France. p. 289.

VOLLENWEIDER, R. A., M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Board Can. 31: 739–762.

VOLLENWEIDER, R. A., W. RAST, AND J. KEREKES. 1980. The phosphorus loading concept and Great Lakes eutrophication, p. 207–234. *In* R. C. Loer, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Pubishers, Inc., Ann Arbor, MI.

WETZEL, R. G. 1981. Longterm dissolved and particulate alkaline phosphatase activity in a hardwater lake in relation to lake stability and phosphorus enrichment. Verh. Int. Ver. Limnol. 21: 337–349.

1983. Limnology. 2nd ed. Saunders College Publishing.

WILLIAMS, J. D. H., J. M. JAQUET, AND R. L. THOMAS. 1976a. Forms of phosphorus in surficial sediments of Lake Erie. J. Fish. Res. Board Can. 33: 413–429.

WILLIAMS, J. D. H., T. P. MURPHY, AND T. MAYER. 1976b. Rates of accumulation of phosphorus forms in Lake Erie sediments. J. Fish. Res. Board Can. 33: 430–439.

WILLIAMS, J. D. H., H. SHEAR, AND R. L. THOMAS. 1980. Availability of *Scenedesmus quadricauda* of different forms of phosphorus in sedimentary materials from the Great Lakes. Limnol. Oceanogr. 251: 1–11.

WORLD HEALTH ORGANIZATION (WHO). 1981. Eutrophication: a global problem. Water Qual. Bull. Part 1 (Vol. 6, No. 3) and Part 2 (Vol. 6. No. 4). World Health Organization, Geneva, Switzerland.

YOUNG, T. C., AND J. V. DEPINTO. 1982. Algal-availability of particulate phosphorus from diffuse and point sources in the lower Great Lakes basin. Hydrobiologia 91: 111–119.

YOUNG, T. C., J. V. DEPINTO, S. E. FLINT, M. S. SWITZENBAUM, AND J. K. EDZWALD. 1982. Algal availability of phosphorus in municipal wastewater. J. Water Polut. Control Fed. 54: 1505–1516.

Epilimnetic Phosphorus Cycling: Influence of Humic Materials and Iron on Coexisting Major Mechanisms[1]

David A. Francko

Department of Botany and Microbiology, Oklahoma State University, Stillwater, OK 74078, USA

Francko, D. A. 1986. Epilimnetic phosphorus cycling: influence of humic materials and iron on coexisting major mechanisms. Can. J. Fish. Aquat. Sci. 43: 302–310.

Two major orthophosphate recycling mechanisms, alkaline phosphatase activity and the photodependent release of P from UV-sensitive complex P, cooccurred in epilimnetic samples from four trophically dissimilar lakes in northcentral Oklahoma. Both of these processes were strongly perturbed upon addition of low concentrations of dissolved humic material (DHM) and ferric iron, alone or in concert, to lake water samples. Planktonic orthophosphate uptake rates were also significantly altered by DHM/Fe addition, and, although the majority of P-uptake was accomplished by cells <3.0 μm in diameter, the effects of DHM/Fe were not size-selective. Additions of DHM/Fe to lake water appeared to promote elevated concentrations of orthophosphate and phosphomonoester substrates of alkaline phosphatase in lake water filtrates. Collectively, these data suggest that epilimnetic P cycling may be viewed as a continuum of processes and that the position of a given lake in the continuum is dynamic and influenced by DHM and Fe.

Deux importants mécanismes de recyclage de l'orthophosphate, soit l'activité de la phosphatase alcaline et le dégagement photo-dépendant de P du complexe P sensible aux rayons ultra-violets, ont eu lieu en même temps dans des échantillons d'eau prélevés dans la zone épilimnétique de quatre lacs de différents niveaux trophiques situés dans le centre-nord de l'Oklahoma. Ces deux processus ont nettement varié suite à l'addition aux échantillons d'eau de faibles concentrations d'humus dissous (DHM) et de fer ferrique, seul ou ensemble. Les taux de captation d'orthophosphate par le plancton ont été aussi modifiés de façon significative par l'apport de DHM/Fe et quoique les cellules mesurant 3,0 μm de diamètre aient absorbé le plus de P, les effets du DHM/Fe n'étaient pas liés à la taille. L'ajout de DHM/Fe à l'eau de lac a semblé favoriser des concentrations élevées d'orthophosphate et de substrats phosphomonoesthers de phosphatase alcaline dans les filtrats d'eau. Ensemble, ces données portent à croire que le cycle de P dans la zone épilimnétique peut être considéré comme un continuum de processus et que l'emplacement d'un lac particulier dans ce continuum est dynamique et qu'il dépend du DHM et du Fe.

Received November 2, 1984
Accepted April 15, 1985
(J8003)

Reçu le 2 novembre 1984
Accepté le 15 avril 1985

Epilimnetic phosphorus cycling, characterized by the transfer of P between various biologically important forms in lake water, the assimilation of ionic orthophosphate (ortho-P; PO_4-P) by bacteria and phytoplankton, and the planktonic release of P-containing compounds back into lake water, remains an incompletely understood process of considerable limnological significance. Because ambient ortho-P concentrations in epilimnetic waters are often insufficient to satisfy planktonic demand (<0.1 $\mu mol \cdot L^{-1}$) (Wetzel 1983; Cembella et al. 1984), attention has focused on mechanisms that might release ortho-P from colloidal P complexes or phosphate esters, thus regenerating free ortho-P for planktonic uptake.

Data in support of three distinct ortho-P regenerative mechanisms have been reported in the literature: (1) displacement and release of ortho-P from a high molecular weight colloidal P fraction (HMWP), which occurs upon polycondensation of a low molecular weight phosphate ester (XP) to HMWP (Lean 1973a, 1973b, 1976; Paerl and Lean 1976; Lean and Nalewajko 1976; Cembella et al. 1984); (2) hydrolysis of dissolved, low molecular weight phosphate esters or HMWP by cell-surface and dissolved alkaline and acid phosphatases, regenerating ortho-P for subsequent uptake (Berman 1970; Heath and Cooke 1975; Paerl and Downes 1978; Francko and Heath 1979, 1981; Rivkin and Swift 1980; Wetzel 1981); and (3) UV light induced release of P from ferric iron – dissolved humic material (DHM) complexes (UV-sensitive complex P) (Koenings and Hooper 1976; Francko and Heath 1979, 1982, 1983; Stewart and Wetzel 1982). Taken together, these reports and others (e.g. Herbes et al. 1975; Wetzel 1983; Olsson and Jansson 1984) suggest that there is no single "epilimnetic phosphorus cycle"; rather, different lake types may either be dominated by one versus another of the three mechanisms described above (a discrete or triad model), or that lakes may be arranged on a continuum, from systems exhibiting one predominant mechanism to those in which features of more than one mechanism cooccur.

In either the discrete or the continuum model, planktonic ortho-P uptake rates and occurrence of each ortho-P regen-

[1]This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

TABLE 1. ^{32}P-uptake rate equations for rapid (0–5 min) and slow (5–60 min) uptake phases in whole lake water samples. Values for the coefficient of determination (r^2) of each equation are given in parentheses.

Lake and date	^{32}P-uptake rate[a]	
	0–5 min	5-60 min
Boomer, 9 Aug. 1984	$\hat{Y} = 0.074 + 0.153X$ (0.979)	$\hat{Y} = 0.417 + 0.071X$ (0.999)
Sangre Isle, 10 Aug. 1984	$\hat{Y} = 1.566 + 3.34X$ (0.968)	$\hat{Y} = 23.743 + 1.25X$ (0.891)
Sanborn, 10 Aug. 1984	$\hat{Y} = -0.973 + 0.763X$ (0.957)	$\hat{Y} = 1.912 + 0.057X$ (0.891)
Theta, 7 Aug. 1984	$\hat{Y} = 0.085 + 0.25X$ (0.985)	$\hat{Y} + 0.808 + 0.106X$ (0.997)

[a]Percent of total ^{32}P added·min^{-1} (N = 5 and 6 for rapid and slow uptake, respectively).

erative mechanism in a given lake system would be strongly influenced by numerous physicochemical variables (Wetzel 1983). However, in the continuum model, the relative importance of cooccurring regenerative mechanisms might be conditionally dependent on the concentration of certain key chemical constituents in lake water; a perturbation in the concentration of such substances could shift the equilibrium in favor of one of the regenerative processes.

Fe–DHM complexes, as noted above, sequester ortho-P into a form that can be made available to plankton via an abiotic process (light irradiation). Stewart and Wetzel (1982) reported that DHM may also affect alkaline phosphatase activity (APA) (biotically mediated P regeneration) in lake water. Thus, DHM and Fe may regulate aspects of both abiotic and biotically mediated P recycling. These relationships can be important both to P cycling and phytoplankton productivity, for major rain events can simultaneously introduce substantial quantities of P and DHM into the epilimnia of small and moderate-sized lakes (Wetzel 1983).

In this study on P recycling in four trophically distinct lakes, I tested the following hypotheses: (1) the uptake of ortho-P by epilimnetic plankton is sensitive to DHM or Fe perturbation, and these effects differ in various planktonic size classes; (2) UV light and APA represent cooccurring ortho-P regenerative mechanisms in these lakes, a thesis in support of the continuum model; and (3) potential ortho-P regeneration from UV irradiation or phosphatase hydrolysis mechanisms may be stimulated or repressed upon experimental manipulation of DHM/Fe concentrations, suggesting that the position of a given lake's P cycling system in the hypothetical continuum is dynamic in nature.

Materials and Methods

Study Sites

For this investigation, I chose four trophically distinct lakes containing low concentrations of DHM and Fe in surface waters (Table 1), and in which high plankton-associated APA and low ionic ortho-P concentrations (suggestive of P-deficient planktonic communities; cf. Heath and Cooke 1975) are typically found in late summer (Francko 1983a, 1984a, 1984b, 1984c). I reasoned that such systems might display more pronounced effects upon DHM/Fe perturbation than stained, bog lakes or lakes with minimal APA.

Epilimnetic water samples were collected from the 0.1-m strata of Sangre Isle Lake, Boomer Lake, Sanborn Lake, and Theta Pond, all located in Payne County, northcentral Oklahoma, during June–August 1984. Sangre Isle Lake is a small (~3.2 ha), shallow (maximum depth ~3.0 m) eutrophic impoundment located in a residential watershed. Boomer Lake (area ~102 ha; mean depth ~3.0 m) is a mesotrophic reservoir containing waters high in clay suspensoids. Sanborn Lake is an oligotrophic natural lake (area ~5 ha; mean depth ~2 m) located in a small forested watershed, so that water clarity remains high (Secchi depth >2 m) during most of the year and the primary production is dominated by submersed and floating-leaved aquatic vascular plants. Theta Pond, located on the Oklahoma State University campus, is a small (~1 ha), culturally eutrophic water body. Further limnological details on these systems may be found in Copeland et al. (1961), Craven and Brown (1968), and Francko (1983a, 1983b; 1984a, 1984b). All water samples were collected in a nonmetallic Van Dorn sampler and were transported back to the laboratory within 30 min of collection.

Orthophosphate Uptake Rate Determinations

Planktonic ortho-P uptake rates were estimated in unamended water samples and in samples amended with DHM, Fe, or KCN. The latter amendment was included because respiratory inhibitors greatly reduce the rate of active P-uptake in some algal species (Rivkin and Swift 1980; Cembella et al. 1984) and because of preliminary evidence suggesting that P-uptake in these lakes may include an important active transport component which is markedly repressed by KCN (R. T. Heath and D. A. Francko, unpubl. data).

Carrier-free, HCl-free ^{32}P-PO_4 (specific activity = 1.3×10^{13} Bq·mg^{-1}) was diluted with sterile, distilled, deionized water to an activity of 3.4×10^6 Bq·mL^{-1}, and 35-μL aliquots were added to 10 mL of whole lake water. In these and subsequent experiments, lake water samples were amended with one of several additions prior to analyses: (1) KCN (50 μL added, final concentration 0.1 mmol·L^{-1}). (2) "Low" or "high" concentrations of DHM (100 or 500 μL, respectively), of purified DHM derived from *Typha* leachate by the dialysis method (3500 dalton nominal molecular weight cutoff) of Stewart and Wetzel (1982). *Typha* leachate is chemically representative of the heterodisperse group of DHM compounds which reach the epilimnia of lakes from plant decomposition processes in adjacent littoral areas. Standard curves relating IR analyses (APHA et al. 1975) of dissolved organic carbon to DHM absorbance in leachate samples (Francko and Heath 1979, 1982) were linear and indicated that the organic carbon as DHM was added to low and high DHM-amended samples at 14 and 70 mg·L^{-1}, respectively. (3) "Low" or "high" amendments of Fe as ferric sulfate (20 or 200 μL of a 5.0 mg·L^{-1} solution in sterile water per 10 mL of lake water, yielding a final addition of Fe of 0.1 or 1.0 mg·L^{-1}). (4) "Low" or "high" amendment of Fe–DHM, produced by simultaneous addition of DHM and Fe solutions as above. Aliquots of filtered lake water were analysed for endogenous Fe and dissolved organic carbon to establish preamendment concentrations of these variables (Table 1; atomic absorption

spectrometry and IR absorption, respectively; APHA et al. 1975).

Amendments of the above solutions were made 1 h prior to addition of ^{32}P-PO_4, and samples were incubated at 22 ± 2°C in an environmental chamber (60 $\mu E \cdot m^{-2} \cdot s^{-1}$) during all analyses. After a 1-h preincubation period, ^{32}P-tracer additions were made to each lake water sample, and 0.5-mL aliquots were withdrawn from each sample at 30 s and 1, 2, 3, 4, 5, 10, 15, 30, and 60 min. Aliquots were filtered through 0.45-μm Millipore filters which had been soaked in 0.5 mol $KH_2PO_4 \cdot L^{-1}$, pH 4.5, to reduce nonspecific binding of label to the filters (R. T. Heath and D. A. Francko 1985), as described, using a Millipore multisample filtration manifold (0.5 atm vacuum differential). Filters were then washed rapidly three times with distilled, deionized water (~7 mL total), placed in glass scintillation vials, dried, and assayed in 5.0 mL of Budget-Solve liquid scintillation cocktail (RPI Corp.). Radioactivity was assayed using a Beckman model 7500 liquid scintillation counter. Aliquots (0.5-mL) of each lake water sample were added directly to scintillation cocktail as a direct measure of total ^{32}P added. Lakewater samples were swirled gently during incubation. Nonspecific filter retention of ^{32}P-PO_4 under the above protocol, as measured in lake water filtrates containing KCN and incubated in P-containing solutions for 1 h, never exceeded 1% of total added DPM, and all uptake data were corrected for nonspecific retention prior to analyses. Other experiments indicated that the filter washing procedure removed <1.0% of label actually incorporated into cells.

The rates of ^{32}P-uptake in unamended and amended samples were used to estimate the effects of DHM and Fe perturbations on the ability of planktonic communities to assimilate ortho-P from solution. KCN additions were used to estimate the sensitivity of uptake processes to respiratory inhibition.

^{32}P-uptake rates were calculated as the percentage of the total radioactivity added that was retained on filters at each time interval. Data sets for each lake water sample and for each amendment described above were subjected to linear regression analyses, and in each case the data residuals demonstrated that uptake was clearly separated into two phases ($P < 0.05$): a rapid uptake phase (0–5 min) and a slow uptake phase (5–60 min). Similar behavior has previously been noted in these lakes (R. T. Heath and D. A. Francko, unpubl. data).

The uptake rate equations for the rapid and slow phases, under each treatment regime and in control samples containing no chemical amendments, were calculated by regression analyses within each time interval. The slopes of ^{32}P-uptake rates in samples containing chemical amendments were compared with the uptake slope in unamended control samples of the same lake water fraction by calculation of a ^{32}P-uptake index, reflecting both repression or stimulation of uptake as a percentage of the unamended control sample so that:

$$\text{Stimulation response (\%)} = (A - C)/A \times 100$$

and

$$\text{Repression response (\%)} = (C - A)/C \times 100$$

where C = slope of uptake rate of the unamended control and A = slope of uptake rate of each amended lake water sample (cf. Francko 1984a, 1984b for discussion of similar indices in nucleotide-induced perturbations of carbon assimilation and APA in phytoplankton). Confidence interval estimates for the value of Y at the midpoints (2.5 and 32.5 min, respectively) of the rapid and slow uptake phases (95% CIE; t-test) were used as an estimate of error in stimulation and repression responses (Zar 1974).

Stewart and Wetzel (1982) reported that the effects of exogenously applied DHM on carbon assimilation rates and APA were more pronounced in smaller size-class (1–5 μm) plankters. Currie and Kalff (1984) have suggested that the majority of P-uptake in epilimnetic communities may be accomplished by small bacterioplankton and algae. Hence, I used size-fractionation techniques to determine whether DHM–Fe effects on P-uptake were found in all size-classes or were restricted to small or large plankton.

Whole water samples from each of the four lakes were incubated with ^{32}P-PO_4 and various chemical amendments as described above. Replicate 0.5-mL aliquots were withdrawn 5 min after ^{32}P addition and were filtered through 0.45- or 1.2-μm Millipore filters or 3.0-μm Nuclepore filters. Thus, these experiments addressed only those effects on the rapid uptake phase. Filtration protocol and methods for determination of radioactivity were identical to that described in the preceding section.

Analytical Methods

The uptake of ortho-P and the potential regeneration of ortho-P via APA are dependent on the concentration of ortho-P and phosphomonoester substrates (PME) of APA, respectively, dissolved in lake water. Both of these P species may be sequestered by DHM–iron complexes, thus altering the availability of P from planktonic utilization (Stewart and Wetzel 1982; Francko and Heath 1983; Wetzel 1983). Orthophosphate (SRP) and PME concentrations in replicates of lake water samples were determined by previously published colorimetric assay techniques (Heath and Cooke 1975; Francko and Heath 1979, 1981). APA in whole lake water and water filtered through 0.45-μm Millipore filters was measured by a fluorometric assay on replicate 4.0-mL samples (*o*-methylfluoroscein phosphate substrate; Perry 1972; Wetzel 1981; Stewart and Wetzel 1982; Francko 1983a, 1984b). Particulate APA was defined as total APA less dissolved activity (Stewart and Wetzel 1982; Francko 1983a). In some experiments, KCN, DHM, and Fe additions were made to lake water samples 1 h prior to APA assay, as described in previous sections; in other experiments, DHM and Fe amendments were added to final concentrations of 143 and 1.0 mg carbon $\cdot L^{-1}$, respectively. Chlorophyll *a* concentrations in lake water samples, corrected for phaeophytin, were measured by a fluorometric technique using acetone extraction (Wetzel and Likens 1979).

The release of SRP by UV-induced photoreduction of Fe–DHM–P complexes was estimated by the method of Francko and Heath (1982, 1983). Ferrous iron concentrations in UV-irradiated and nonirradiated lake water samples were measured by a bathophenanthroline method (absorbance at 533 nm, calibrated with ferrous sulfate standard; Stumm and Lee 1961; Francko and Heath 1982, 1983). Lake water samples were alternately adjusted to pH 4.5 with the addition of potassium acetate buffer (0.1 mol $\cdot L^{-1}$) and amended with bathophenanthroline reagents prior to irradiation with UV light or pH adjustment, and reagent additions were made immediately after the irradiation period. DHM concentrations in 0.45-μm-filtered lake water samples and *Typha* dialysates were calculated by a standard curve relating light absorbance at 400 nm (Francko and Heath 1979, 1982, 1983) to the concentration of dissolved organic carbon as measured by IR analysis (APHA et al. 1975).

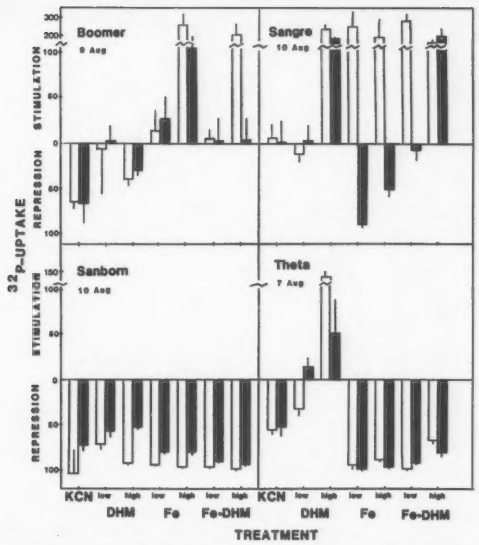


FIG. 1. Percentage stimulation or repression of rapid (0−5 min) and slow (5−60 min) ^{32}P-uptake rates (open and solid bars, respectively) in lake water aliquots amended with various treatments as compared with an unamended control. Error bars denote 95% confidence interval of $\hat{Y}$ calculated at the midpoint of the rapid or slow uptake phase.

TABLE 2. Physicochemical and algal community variables. Values in parentheses denote ±SD (N = 3). DHM contained 2.6 μg SRP·L^{-1} and 0.7 μg PME·L^{-1}. Ferric sulfate solution contained 0.2 μg SRP·L^{-1} and 0.2 μg PME·L^{-1}.

Lake and date	pH	Chl *a* (μg·L^{-1})	DOC (μg·L^{-1})	Fe (μg·L^{-1})
Theta, 7 Aug. 1984	7.82	2.1(0.2)	21(7)	0.033
Boomer, 9 Aug. 1984	7.85	2.5(0.4)	78(10)	0.370
Sanborn, 10 Aug. 1984	7.69	1.0(0.1)	71(6)	0.050
Sangre, 10 Aug. 1984	8.22	40.0(1.5)	100(20)	0.060
DHM solution	8.00	—	1430(70)	0.020
Ferric sulfate	8.00	—	—	1.000

NOTE: Algal genera in order of importance: Theta Pond (8.1 × 10^5 cells·mL^{-1}): microflagellates, *Chroococcus*, *Scendesmus*, *Closterium*, unidentified green unicells; Boomer Lake (3.1 × 10^6 cells·mL^{-1}): microflagellates, *Chroococcus*, unidentified nonmotile green unicells; Sanborn Lake (1.5 × 10^5 cells·mL^{-1}): microflagellates and other unidentified small green unicells, occasional *Selenastrum*; Sangre Isle Lake (2.8 ± 10^6 cells·mL^{-1}): *Aphanazomenon*, *Anabaena*, *Chroococcus*, small unidentified green unicells and microflagellates.

Results

P-Uptake Analyses

My results support the view that planktonic P-PO_4 uptake in each of the four lakes was sensitive to DHM and Fe additions, both alone or in concert. P-uptake rate equations for rapid (0−5 min) and slow (5−60 min) uptake phases in chemically unaltered water, shown in Table 2, demonstrate that <10% of

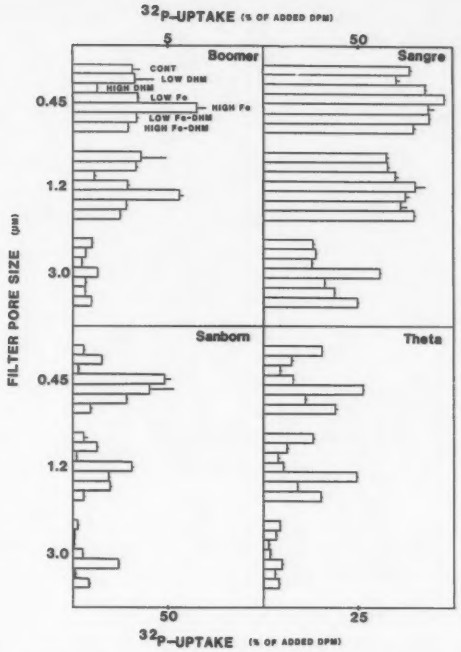


FIG. 2. Uptake of radiolabeled phosphate during the rapid uptake phase by various particule size-classes, 15 August 1984, as a percentage of the total radioactivity added. Error bars denote ±SD of replicate determinations under a variety of treatment amendments.

the P-tracer was assimilated within 60 min by the plankton in Boomer Lake, Theta Pond, and Sanborn Lake samples, while >90% of the label was associated with cells after 60 min in Sangre Isle Lake samples.

Each lake exhibited different responses to additions of DHM and Fe (Fig. 1). In oligotrophic Sanborn Lake, all additions of DHM or Fe, alone or in combination, strongly repressed P-uptake, and, with the exception of the high DHM treatment, samples from eutrophic Theta Pond responded similarly. In Boomer Lake samples and samples from eutrophic Sangre Isle Lake, certain amendments were associated with enhanced P-uptake capacity, especially in the rapid phase. In several cases, uptake rates were more than twofold higher in lake water samples containing added Fe or DHM. However, the slow uptake phase was strongly inhibited by Fe alone in Sangre Isle Lake samples. In the majority of cases, the data indicate that the sum of individual effects of Fe or DHM alone on P-uptake was a reasonably accurate indicator of the effects noted when combined additions of high or low Fe−DHM were employed.

In three of the lakes (Boomer, Sanborn, and Theta), KCN additions strongly repressed P-uptake, suggesting that at least a portion of P-uptake in these systems may be energey dependent. In Sanborn Lake samples, particularly, which were also strongly repressed by either Fe or DHM additions, KCN data indicate that the former substances may perturb active P-uptake processes. However, the minimal effects of KCN additions on Sangre Isle Lake samples, coupled with the marked effects of DHM/Fe, support the opposite view, namely that DHM/Fe may interact with KCN-insensitive uptake processes.

Data on the size-selective effects of DHM or Fe amendments (Fig. 2) demonstrate two main points: (1) in each of the four

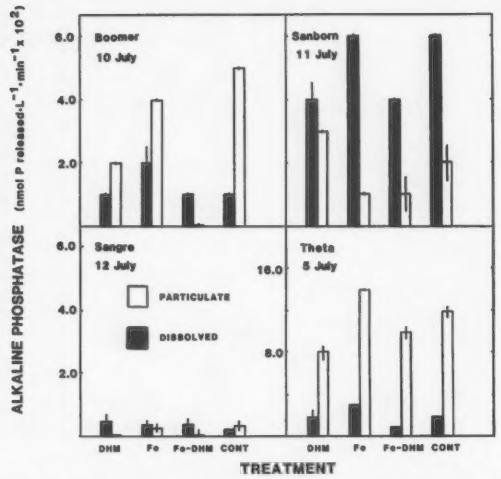


FIG. 3. Particulate-associated and dissolved APA in lake water samples amended with *Typha* DHM (143 mg added·L^{-1}), ferric sulfate (1.0 mg Fe added·L^{-1}), or both DHM and Fe, as compared with-unamended samples. Error bars denote ±SD of replicate determinations.

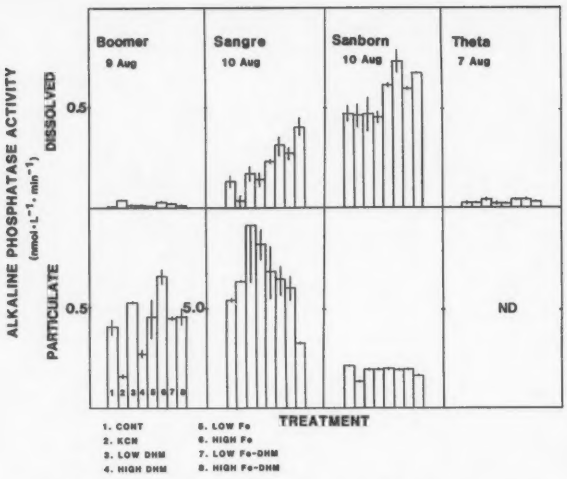


FIG. 4. Dissolved and particulate-associated APA in lake water samples under a variety of chemical amendments and in unamended control samples. Error bars denote ±SD of replicate determinations. ND = none detected.

lakes, <50% of the total ^{32}P-uptake was retained by 3.0-μm filters in unamended lakewater aliquots, suggesting that uptake by small particles comprised an important portion of total P-assimilation in each of the lakes and (2) the effects of DHM and Fe on P-uptake rates were not size-specific. I observed that microflagellate algae and other very small unicellular green and blue-green algae (~1 μm or less in diameter) comprised a significant proportion of the phytoplankton in samples from each of these four lakes (Table 1). The importance of small particles <3.0 μm in size to total P-uptake was especially prominent in samples from Sangre Isle Lake, where long filaments of *Aphanizomenon* comprised over 60% of the total phytoplankton counts and ~95% of the algal biomass (estimated from average sizes of filaments), yet less than half of the P-uptake was accounted for in the 3.0-μm size-class.

With only a few exceptions, there was little qualitative difference between the P-uptake responses of the three particle size-classes upon similar addition of DHM or Fe, regardless of the lake water sample analyzed (Fig. 2). Exceptions to this generalization include (1) the strong repression of uptake in the 3.0-μm size-class (Sanborn) upon addition of low DHM, compared with either of the smaller size-classes, where the same DHM addition stimulated P uptake, (2) the slight repression of uptake upon low DHM addition in 0.45-μm particles (Sangre), compared with controls, versus the lack of such an effect upon low DHM addition in the 1.2-μm size-class, and (3) differences in the effects of low and high DHM, low Fe, and high Fe−DHM in the 3.0-μm size-class (Sangre) versus comparable experimental conditions in either of the smaller size-classes.

Effects of DHM and Fe on APA

My data on APA in these four lakes and its sensitivity to DHM and Fe support these views: (1) APA represented a major potential P-regenerative mechanism in each lake during the investigation period; (2) both dissolved and particulate APA may be strongly influenced by DHM or Fe concentrations in lake water; and (3) APA may either be stimulated or repressed by additions of DHM or Fe to lake water samples; the degree of stimulation or repression noted was sufficient to affect the relative importance of APA as a P-regenerative mechanism. In a preliminary series of experiments, conducted prior to P-uptake work described earlier, I amended lake water samples with dissolved organic carbon (143 mg·L^{-1} as DHM) or 1.0 mg Fe·L^{-1}), alone or in concert (Fig. 3). Each lake varied in both total APA and in the proportion of particulate-associated versus dissolved APA, in agreement with previous work on these systems (Francko 1983a). In oligotrophic Sanborn Lake, which had the highest total APA of the four systems, dissolved APA which was strongly repressed by DHM or Fe−DHM predominated; Fe alone did not affect activity. Proportionately less dissolved APA was noted in samples from the other three lakes, and DHM or Fe additions produced few effects on dissolved APA.

Particulate APA in each lake was strongly repressed by DHM and Fe−DHM in samples from all lakes but Sanborn; in the latter lake, Fe alone and Fe−DHM repressed APA. In Boomer Lake samples, DHM addition reduced particulate APA to <40% of the unamended control value, and Fe−DHM addition reduced activity to an undetectably low level.

In order to test the validity of these observations and to relate APA effects to P-uptake effects, I repeated these experiments on subsamples of water which was also used for P-uptake experiments (Fig. 4). As in the P-uptake series, I used stepwise additions of DHM and Fe, alone or in concert. APA in Theta Pond water, which consisted entirely of dissolved activity, was unaffected by any amendment used. In Sanborn samples, the majority of APA was found in the dissolved phase, and activity was stimulated by low/high Fe or Fe−DHM; DHM alone and KCN did not affect dissolved activity, and KCN was the only addition to affect particulate activity. In the 10 August sample from Sangre Isle Lake, total and particulate APA were the highest I have recorded in several years of monitoring on this

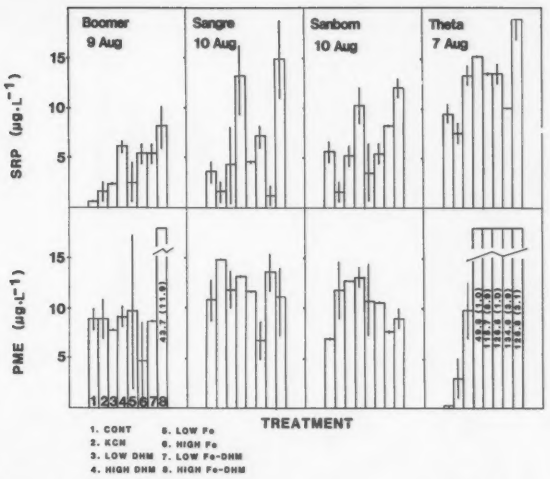


FIG. 5. Concentrations of SRP and PME in lake water filtrates after 1 h of incubation of whole water samples with various additions of DHM, KCN, or ferric sulfate, as compared with values of unamended controls. Error bars and values in parentheses denote ±SD of replicate determinations.

lake (Francko 1983a, 1984b, 1984c). Dissolved APA in this system was unaffected by low/high DHM alone, repressed by KCN, and stimulated by Fe alone or Fe−DHM. Particulate APA in Sangre Isle samples was strongly repressed by high Fe−DHM, but was stimulated by low/high DHM alone and by KCN. KCN and high DHM repressed activity in Boomer Lake samples, while high Fe addition was stimulatory.

Effects of KCN, DHM, and Fe on SRP and PME Concentrations

DHM and Fe−DHM complexes are known to sequester ortho-P, thus altering the amount of P available for plankton uptake (Wetzel 1983). In lake water samples from each of the four systems, I found that high additions of DHM alone or Fe−DHM consistently yielded higher SRP concentrations than in unamended water samples (Fig. 5). Fe additions alone also promoted a similar effect, although the differences were not as great. Although such results can be interpreted several ways, they are consistent with the view that added Fe−DHM complexed naturally occurring ortho-P into a form which was chemically reactive but not biologically available, so that it could accumulate to higher concentrations. The minimal contaminating additions of SRP present in Fe or DHM stock solutions (Table 1) were corrected for prior to presentation of data in Fig. 5. In each lake sample, the resultant SRP concentrations after 1 h in high Fe−DHM-containing lake water was elevated at least twofold to concentrations suggestive of much more eutrophic systems. These data, in concert with P-uptake and APA experiments on the same sampling dates, further support the thesis that Fe/DHM may affect several aspects of P recycling. Samples from Sanborn Lake were the only ones containing significanty reduced SRP after KCN incubation, suggesting that the above processes were not greatly affected by inhibition of community respiration.

PME concentrations in waters from Theta pond were strongly elevated in samples containing Fe and DHM additions (Fig. 5). High Fe−DHM addition to Boomer water was also associated with greatly increased PME. These data do not represent artifacts; a second series of samples from Boomer and Theta, which were prepared and analyzed as above, yielded statistically similar results (t-test; $P < 0.05$). In Sangre Isle and Sanborn samples, Fe/DHM effects on PME were much less pronounced. Data on the effects of DHM or Fe on PME are important because the biological significance of APA as a P recycling mechanism is dependent on the amount of substrate available in lake water as well as enzymatic activity (Heath and Cooke 1975). The data suggest that, like SRP, PME may become associated with Fe−DHM complexes via an abiotic process, thus limiting hydrolysis by APA, a thesis consistent with a previous report by Stewart and Wetzel (1982). Alternatively, because whole water samples were incubated with DHM, etc., these substances may have altered the rate of SRP release from plankton, or, by repressing APA activity or P-uptake, promoted accumulation of PME or SRP, respectively.

UV-Sensitive P Release and Photoreduction of Ferric Iron

The hypothesized continuum model of P recycling predicts that, in addition to APA and hydrolyzable substrates of APA, measurable quantities of UV-sensitive P should also be found in epilimnetic waters. If the relative importance of UV light as a P recycling mechanism is dependent on Fe−DHM in lake water, as suggested by Francko and Heath (1979, 1982, 1983), additions of Fe or DHM to lake water samples should increase the amount of UV-sensitive P, thus changing the "position" of the lake's P cycle in the hypothetical continuum.

My data support the plausibility of the continuum model. Small amounts of additional SRP were released upon UV irradiation in Sangre, Theta, and Boomer waters (Fig. 6). The total increase in filtrate SRP relative to amounts present prior to irradiation were modest, ranging from a 10% increase in Boomer water to 26 and 33% increases in Sangre and Theta water, respectively. However, with the exception Sangre Isle samples, 90 min of irradiation did not result in further increases in SRP, and Sanborn Lake samples actually contained less SPR after irradiation than did unirradiated control samples. There appeared to be little relationship between irradiation and the ferrous iron content or absorbance at 400 nm of waters for many of the lakes. Francko and Heath (1979, 1982, 1983) reported that in a darkly stained bog lake, UV irradiation resulted in a first-order relationship between the conversion of Fe^{3+} to Fe^{2+} and the release of SRP from high molecular weight Fe−DHM complexes as well as parallel losses in DHM absorbance.

Additional experiments on the degree to which photodependent processes could be perturbed upon additions of DHM and ferric iron to lake water samples (Fig. 7) were consistent with the dynamic view of the continuum model, but the results were much less dramatic than in similar experiments on APA perturbation described earlier. In Theta Pond samples adjusted to pH 4.5 prior to UV irradiance (Fig. 7A), net UV-sensitive P release (SRP in irradiated samples minus that in dark control, corrected for initial SRP concentration at time zero) was markedly higher in samples amended with DHM, ferric iron, or Fe−DHM after 30 min of irradiation than in the unamended control sample. The data suggest that during the 1-h dark preincubation period prior to illumination with UV light, more P was sequestered into a form, reactive as SRP only after irradiation, when additional Fe−DHM was supplied in the filtrate.

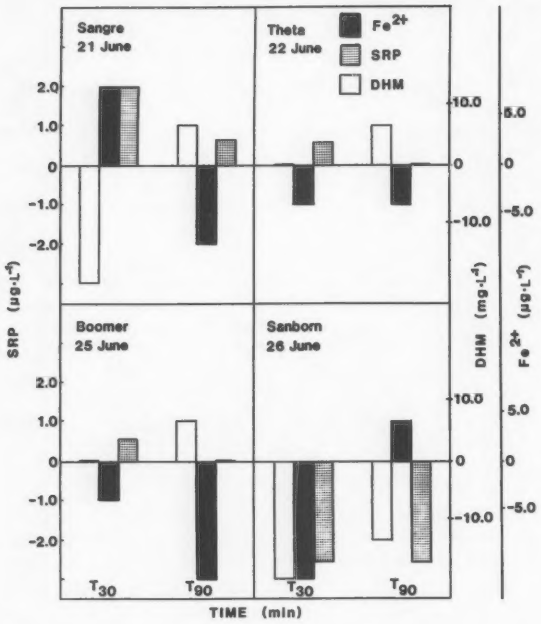


FIG. 6. Net changes in SRP, DHM, and ferrous iron content of lake water filtrates irradiated with low-dose UV light, as a function of irradiation time. All values are corrected for initial concentrations and for the values of dark-incubated control aliquots of the same lake water samples.

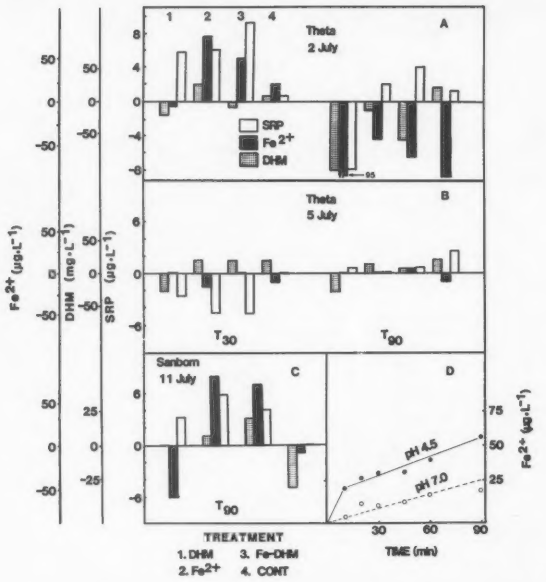


FIG. 7. Net changes in SRP, DHM, and ferrous iron concentrations in lake water samples amended with DHM (143 mg added·L^{-1}), ferric sulfate (1.0 mg Fe added·L^{-1}), or both DHM and Fe, upon irradiation with low-dose UV light for various time intervals. All values were corrected for initial concentrations and for the concentrations in dark-incubated aliquots which were analyzed simultaneously. Figures 7A and 7C represent lake water samples adjusted ot pH 4.5 and containing Fe reagents at the start of the irradiation period; Fig. 7B samples were irradiated at the natural lake water pH, and adjustment to pH 4.5 and addition of Fe reagents was made after irradiation; Fig. 7D denotes photoreduction kinetics of 0.1 mg ferric sulfate·L^{-1} as a function of pH.

Because the above processes occurred in filtered lake water, it is likely that the mechanisms may be abiotic in nature, although the potential presence of organisms capable of passing through the 0.45-µm Millipore filters was not investigated. Some of the Fe added in the ferric form was also photoreduced by UV light during the first 30 min.

However, after 90 min of irradiation, Theta Pond samples displayed less defined properties (Fig. 7A). In samples containing Fe or Fe−DHM additions, UV-sensitive P concentrations remained elevated above those of the control sample which received no additional amendment, but the increase was much less pronounced than that at 30 min. There was also less DHM absorbance in irradiated samples which received additional DHM amendments compared with darkened control samples. However, ferrous iron concentrations in each irradiated sample were actually lower than in corresponding dark-incubated control samples. While the samples amended with additional Fe displayed less negative values, these data are difficult to resolve with the hypothesis that a direct relationship existed between Fe photoreduction and SRP release.

In Sanborn Lake samples (Fig. 7C), ~19.9 µg SRP·L^{-1} was present in filtrates prior to irradiation. No UV-sensitive P was released in unamended irradiated samples. However, ~3−6 µg UV-sensitive P·L^{-1} was produced upon irradiation of aliquots amended with DHM, Fe, or Fe−DHM and a relationship between Fe photoreduction and SRP release was noted in samples amended with additional ferric iron prior to irradiation. Such data suggest that the influx of DHM/Fe into a lake system, e.g during a storm event, may introduce the UV-light dependent P recycling process to epilimnetic waters previously lacking this mechanism.

The magnitude of photodependent P recycling processes may be markedly influenced by pH. When Theta Pond samples were amended with Fe and DHM as above and irradiated at the nominal pH of the lake (pH 7.0), rather than pH 4.5 as in Fig. 7A and 7C, and adjustment to pH 4.5, with concomitant addition of bathophenanthroline reagents, was made after the irradiation period, unamended control aliquots actually contained more UV-sensitive P than did amended aliquots (Fig. 7B). Similarly, the photoreduction of Fe and loss of DHM absorbance were much less pronounced. Consistent with this view, the photoreduction of stock solutions of ferric sulfate (Fig. 7D) was much more rapid at pH 4.5 than at pH 7.0.

The bathophenanthroline method requires an acidic pH for colorimetric determination of ferrous iron and the ferrous ion is much more stable at acidic pH in epilimnetic waters (Koenings and Hooper 1976). Still, it is clear that incubation of samples at acidic pH during irradiation greatly overestimated the rate of UV-sensitive P photorelease which would occur at the normal pH of these lakes in nature. While the data are not shown, I conducted additional experiments on Boomer Lake and Sangre Isle Lake waters during July 1984 (three analyses on each lake). When pH adjustments were made (to pH 4.5) prior to irradiation, a maximum of 3.9 µg additional UV-sensitive P·L^{-1} was formed in Sangre Isle Lake water upon simultaneous addition of both Fe and DHM, while no detectable UV-sensitive P was found in Boomer water. When aliquots

were irradiated at the normal pH of the lake water, a maximum of 2.0 μg additional UV-sensitive $P \cdot L^{-1}$ was formed in Sangre Isle Lake, while the same P fraction remained at undetectable concentrations in Boomer Lake.

Discussion

Collectively, the above data supported the following theses: (1) planktonic ortho-P uptake rates are strongly modulated by extant Fe and DHM in eplimnetic waters, and such effects are not confined to small versus large plankters, even in systems where much of the total P-uptake is by small cells; (2) two ortho-P regenerative mechanisms (APA and UV-light photorelease) may cooccur in epilimnetic waters, in support of the continuum hypothesis of P recycling; (3) both of these P-regenerative mechanisms may be strongly repressed or stimulated by Fe/DHM, so that the relative importance of each mechanism and the "position" of a given lake in the hypothetical continuum are dynamic; and (4) Fe/DHM additions are associated with elevated concentrations of ortho-P and PME in lake water, so that the amount of P available for planktonic uptake is greatly altered.

Such broad effects on several aspects of the P cycle were noted upon relatively modest perturbation of extant Fe or DHM concentrations (Table 1), reflecting events that might occur in situ (e.g. during a storm event). The dissolved organic carbon data for lakewater samples, as a measure of all organic carbon constituents, represent a gross overestimate of DHM in these waters. In unstained waters, humic acid concentrations generally range between 1 and 10 $mg \cdot L^{-1}$ (cf. Martin and Pierce 1971; Visser 1984). Based on dissolved organic carbon data and on the estimate of Reuter and Perdue (1977) that humic materials account for about 60% of the total dissolved organic carbon in most freshwaters, the addition of DHM to lakewater aliquots resulted in an increase of ~23–111% (at additions of 14 $mg \cdot L^{-1}$), ~117–556% (at additions of 70 $mg \cdot L^{-1}$), or ~238–1135% (at additions of 143 $mg \cdot L^{-1}$) in the final concentration of DHM prior to ^{32}P addition, depending on the lakewater sample analyzed. While these figures are subject to considerable error, in no case did final DHM concentrations approach those commonly found in stained bog waters, which often exceed 0.5 $g \cdot L^{-1}$ (cf. Reuter and Perdue 1972). Based on the concentrations of dissolved Fe in waters from each lake shown in Table 1, the addition of 0.1 or 1.0 mg of ferric iron to some lake water aliquots resulted in a similar degree of perturbation in extant Fe levels.

Although my data were limited to only a few sampling dates on each lake, they suggest that DHM/Fe may be involved in several aspects of the epilimnetic P cycle and that such effects may vary in lakes of differing trophic status. For example, in unproductive Sanborn Lake samples collected on 10 August, high Fe–DHM addition (1) strongly repressed P uptake, (2) stimulated dissolved APA, and (3) increased the amount of ortho-P and PME found in filtrates. On a different sampling date (11 July), high Fe–DHM apparently sequestered P into a UV-sensitive P fraction not found in samples lacking Fe–DHM addition. Taken together, such findings predict that an influx of Fe–DHM to Sanborn waters would result in elevated ortho-P in these waters, but a diminished ability of plankton to utilize this resource, thus further reducing planktonic primary production in this oligotrophic system. In an extreme example of this view, highly stained bog systems frequently exhibit lower primary production rates than would be predicted based on ortho-P content of the epilimnia (Wetzel 1983). Further, Stewart and Wetzel (1982) have reported that planktonic primary production in unstained systems may be inhibited by DHM addition.

In eutrophic Sangre Isle Lake samples, in which P-uptake rates were rapid, Fe–DHM further stimulated P-uptake and dissolved APA, and increased the amount of ortho-P and UV-sensitive P in lake water. All of the above would be expected to enhance P-acquisition by plankton, thus further stimulating primary production. Similarly, DHM and Fe affected several aspects of P-acquisition in Boomer Lake and Theta Pond samples.

The mechanisms underlying the processes described in this paper can only be speculated on at this time. The binding of orthophosphate and perhaps organophosphates to Fe–DHM complexes in acidic lake water has been described by several workers (reviewed by Stewart and Wetzel 1982). In aerobic water from an acidic lake, however, the interaction between colloidal organic matter and Fe was found to decrease phosphate adsorption onto Fe–organic complexes, thus freeing inorganic P for phytoplanktonic utilization (Koenings and Hooper 1976). Binding of P occurred when Fe was present in the ferric state; ferrous iron – DHM complexes could not bind P. Concomitantly, Jansson (1981) has shown that Al and Fe are capable of inhibiting naturally occurring APA and that both metals have an affinity for PME which forces competitive inhibition between metals and phosphatase for dissolved substrate. When APA was unsaturated, as is the case in most natural waters, Jansson found that the inhibitory effects of Al were independent of substrate concentration. Few studies on the effects of Fe on P-uptake have been conducted (reviewed by Cembella et al. 1984). Such studies would appear to be of particular importance in view of recent evidence that P transport may be mediated by both electrogenic and nonelectrogenic ion pumps, which might be metal- or DHM-sensitive (Cembella et al. 1984).

In summary, it appears that epilimnetic P cycling, as a summation of the uptake, sequestering, and release of poorly characterized compounds, and involving biotic and abiotic processes which appear to be modulated by organic and inorganic constituents of lake water, is not readily characterized by any single process. Rather, the data presented in this paper and those published by a large number of investigators may best be resolved by postulating that P recycling represents a continuum of processes, involving abiotic complexation and release, and a number of biotic processes involving enzymatic hydrolysis, each of which is highly plastic in the natural environment.

Acknowledgements

This work was supported by grants from the National Science Foundation (BSR-8214577) and a State of Oklahoma Regents Water Grant. Partial travel support and publication costs were provided by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI 48104. I also acknowledge the extensive technical assistance of Mr. Steve Nolen, the assistance of Brock University, St. Catharines, Ont., and the coorganizers of the Phosphorus–Plankton Dynamics Symposium, Drs. Stephen Tarapchak and Czesia Nalewajko.

References

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1975. Standard

methods for the examination of water and wastewater. 14th ed. Washington, DC. 1193 p.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

CEMBELLA, A. D., N. J. ANTIA, AND P. J. HARRISON. 1984. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective: Part 1, p. 317–391. *In* W. M. O'Leary [ed.] CRC Critical reviews in microbiology. Vol. 10(4). CRC Press, Inc., Boca Raton, FL.

COPELAND, B. J., J. L. BUTLER, AND W. L. SHELTON. 1961. Photosynthetic productivity in a small pond. Proc. Okla. Acad. Sci. 52: 22–26.

CRAVEN, R. E., AND B. E. BROWN. 1968. Physicochemical conditions of Boomer Lake, Payne County, Oklahoma. Proc. Okla. Acad. Sci. 59: 23–29.

CURRIE, D. J., AND J. KALFF. 1984. The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in freshwater. Limnol. Oceanogr. 29: 311–321.

FRANCKO, D. A. 1983a. Size-fractionation of alkaline phosphatase activity in lake water by membrane filtration. J. Freshwater Ecol. 2: 305–309.

1983b. Dissolved cyclic adenosine 3′:5′-monophosphate (cAMP) in a eutrophic reservoir lake. Proc. Okla. Acad. Sci. 63: 9–11.

1984a. Phytoplankton metabolism and cyclic nucleotides: I. Nucleotide-induced perturbations of carbon assimilation. Arch. Hydrobiol. 100: 341–354.

1984b. Phytoplankton metabolism and cyclic nucleotides: II. Nucleotide-induced perturbations of alkaline phosphatase activity. Arch. Hydrobiol. 100: 409–421.

1984c. Relationships between phosphorus functional classes and alkaline phosphatase activity in reservoir lakes. J. Freshwater Ecol. 2: 541–547.

FRANCKO, D. A., AND R. T. HEATH. 1979. Functionally distinct classes of complex phosphorus compounds in lake water. Limnol. Oceanogr. 24: 463–473.

1981. Aluminum sulfate treatment: short-term effect on complex phosphorus compounds in a eutrophic lake. Hydrobiologia 78: 125–128.

1982. UV-sensitive complex phosphorus: association with dissolved humic material and iron in a bog lake. Limnol. Oceanogr. 27: 564–569.

1983. Abiotic uptake and photodependent release of phosphate from high-molecular-weight humic–iron complexes in a bog lake, p. 467–480. *In* R. F. Christman and E. Gjessing [ed.] Aquatic and terrestrial humic materials. Ann Arbor Science Publishers, Ann Arbor, MI.

HEATH, R. T., AND G. D. COOKE. 1975. The significance of alkaline phosphatase in a eutrophic lake. Verh. Int. Ver. Limnol. 19: 959–965.

HERBES, S. E., H. E. ALLEN, AND K. H. MANCY. 1975. Enzymatic characterization of soluble organic phosphorus in lake water. Science (Wash., DC) 197: 432–434.

JANSSON, M. 1981. Induction of high phosphatase activity by aluminum in acid lakes. Arch. Hydrobiol. 93: 32–44.

KOENINGS, J. P., AND F. HOOPER. 1976. The influence of colloidal organic matter on iron–phosphorus cycling in an acid bog lake. Limnol. Oceanogr. 21: 684–696.

LEAN, D. R. S. 1973a. Phosphorus dynamics in lakewater. Science (Wash., DC) 179: 678–680.

1973b. Movements of phosphorus between its biologically important forms in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

1976. Phosphorus kinetics in lake water: influence of membrane filter pore size and low pressure filtration. J. Fish. Res. Board Can. 33: 2800–2804.

LEAN, D. R. S., AND C. NALEWAJKO. 1976. Phosphate exchange and organic phosphorus excretion by freshwater algae. J. Fish. Res. Board Can. 33: 1312–1323.

MARTIN, D. F., AND R. H. PIERCE. 1971. A convenient method for the analysis of humic acid in fresh water. Environ. Lett. 1: 49–52.

OLSSON, H., AND M. JANSSON. 1984. Stability of dissolved [32]P-labelled phosphorus compounds in lake water and algal cultures — resistance to enzymatic treatment and algal uptake. Verh. Int. Ver. Limnol. 22: 200–204.

PAERL, H. W., AND M. T. DOWNES. 1978. Biological availability of low versus high molecular weight reactive phosphorus. J. Fish. Res. Board Can. 35: 1639–1643.

PAERL, H. W., AND D. R. S. LEAN. 1976. Visual observations of phosphorus movement between algae, bacteria, and abiotic particles in lake waters. J. Fish. Res. Board Can. 33: 2805–2813.

PERRY, M. J. 1972. Alkaline phosphatase in subtropical Central North Pacific waters using a sensitive fluorometric method. Mar. Biol. 15: 113–119.

REUTER, J. H., AND E. M. PERDUE. 1972. Chemical characterization of dissolved organic matter and its influence on the chemistry of river water. Completion report OWRR Project No. A-026-GA., School of Geophysical Sciences, Georgia Institute of Technology, Atlanta, GA.

1977. Importance of heavy metal – organic matter interactions in natural water. Geochim. Cosmochim. Acta 41: 325–334.

RIVKIN, R. B., AND E. SWIFT. 1980. Characterization of alkaline phosphatase and organic phosphorus utilization in the oceanic dinoflagellate *Pyrocystis noctiluca*. Mar. Biol. 61: 1–8.

STEWART, A. J., AND R. G. WETZEL. 1982. Influences of dissolved humic materials on carbon assimilation and alkaline phosphatase in natural algal–bacterial assemblages. Freshwater Biol. 12: 369–380.

STUMM, W., AND G. F. LEE. 1961. Oxygenation of ferrous iron. Ind. Eng. Chem. 52: 143–146.

VISSER, S. A. 1984. Seasonal changes in the concentration and colour of humic substances in some aquatic environments. Freshwater Biol. 14: 79–87.

WETZEL, R. G. 1981. Longterm dissolved and particulate alkaline phosphatase activity in a hardwater lake in relation to lake stability and phosphorus enrichments. Verh. Int. Ver. Limnol. 21: 337–349.

1983. Limnology. 2nd ed. Saunders, Philadelphia, PA. 767 p.

WETZEL, R. G., AND G. LIKENS. 1979. Limnological analyses. Saunders, Philadelphia, PA. 358 p.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 p.

Does Algal–Bacterial Phosphorus Partitioning Vary Among Lakes? A Comparative Study of Orthophosphate Uptake and Alkaline Phosphatase Activity in Freshwater[1,2]

David J. Currie[3]

Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succursale "A", Montréal, Qué. H3C 3J7

and Ellen Bentzen[4] and Jacob Kalff

Department of Biology, McGill University, 1205 Avenue Dr. Penfield, Montreal, Que. H3A 1B1

Currie, D. J., E. Bentzen, and J. Kalff. 1986. Does algal–bacterial phosphorus partitioning vary among lakes? A comparative study of orthophosphate uptake and alkaline phosphatase activity in freshwater. Can. J. Fish. Aquat. Sci. 43: 311–318.

In order to distinguish the activity of phytoplankton and bacterioplankton in 13 lakes of widely varying trophy, we size-fractionated orthophosphate uptake and alkaline phosphatase activity. In most lakes, orthophosphate uptake was consistently and overwhelmingly associated with the smallest particles. Based upon indicators of algal and bacterial presence in each size class, we inferred that the bacterioplankton are responsible for ≥95% of the orthophosphate uptake in situ, except in lakes that are not phosphorus-deficient. In contrast, a large portion of the alkaline phosphatase activity was free in solution (median 46%), and much of the remainder (median 44%) was apparently associated with algae.

Afin de différencier l'activité du phytoplancton et du bactérioplancton dans 13 lacs montrant des niveaux variables d'apports en nutriments, les auteurs ont fractionné la captation d'orthophosphate et l'activité de la phosphatase alcaline selon la taille des particules. Dans la plupart des lacs, la captation d'orthophosphate était uniformément et complètement associée aux plus petites particules. D'après des indicateurs de la présence d'algues et de bactéries appartenant à chaque classe de taille, ils ont déduit que le bactérioplancton effectuait 95 % ou plus de la captation in situ d'orthophosphate, sauf dans les lacs sans carence en phosphore. Par contre, une grande partie de la phosphatase alcaline était libre en solution (médiane : 46 %) et le reste (médiane : 44 %) était apparemment associé avec des algues.

Received July 18, 1984
Accepted January 29, 1985
(J7868)

Reçu le 18 juillet 1984
Accepté le 29 janvier 1985

What regulates the dynamics of phytoplankton in situ? It is now generally accepted that phytoplankton growth and production in temperate zone lakes are most often phosphorus limited (Schindler 1977; Kalff and Knoechel 1978). Further, it is believed that orthophosphate is the form of phosphorus that is most available to the phytoplankton (Wetzel 1983; Goldman and Horne 1978; Nalewajko and Lean 1980). These two ideas have underlain most research on the growth of freshwater plankton in recent years.

In contrast, the earliest studies of phosphorus cycling in situ suggested that bacteria, not phytoplankton, might be largely responsible for orthophosphate uptake (Rigler 1956; Hayes and Phillips 1958). Currie and Kalff (1984b) tested this hypothesis by partitioning orthophosphate uptake in Lake Memphremagog, Quebec, into two size classes. They found that very little orthophosphate uptake was traceable to particles larger than 3.0 μm, and they concluded that bacterioplankton were responsible for virtually all the uptake of orthophosphate. Other data exist that are consistent with this conclusion (Rigler 1956; Burnison 1975; Berman and Stiller 1977; Koschel 1980). However, R. Moll and S. J. Tarapchak (G.L.E.R.L., NOAA, Ann Arbor, MI; abstract presented at 1983 annual meeting of the International Association for Great Lakes Research) recently reached the opposite conclusion based upon experiments in Lake Michigan, and Paerl and Lean (1976) and Berman (1985) have observed mixed algal and bacterial uptake. Which organisms get the orthophosphate? The question here is of fundamental importance, for if phytoplankton uptake of orthophosphate is negligible, then the ubiquitous hypothesis that phytoplankton growth depends upon orthophosphate (e.g. Tilman 1977; Cemballa et al. 1984b) is in serious doubt.

A potential alternative source of phosphorus for phytoplankton is dissolved organic phosphorus (DOP). At least some DOP

[1]Parts of this paper were presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

[2]A contribution of the Limnology Research Centre, McGill University, and the Groupe d'Ecologie des Eaux Douces, Université de Montréal.

[3]Present address: Department of Biology, University of Ottawa, Ottawa, Ont. K1N 6N5.

[4]Present address: Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1.

TABLE 1. Location, surface area, Secchi depth, and chlorophyll concentration (±95% C.I.) of the lakes included in this study.

Lake	Sampling location N	Sampling location W	Area (km^2)	Secchi (m)	Chlorophyll ($\mu g \cdot L^{-1}$)
Brome	45°14′	72°30′	14.3	3.7	5.7±0.5
Massawippi	45°19′	72°03′	10.9	3.7	2.3±0.5
Orford	45°18′	72°02′	1.3	5.6	1.3±0.4
Waterloo	45°20′	72°31′	1.78	0.8	44.1±12.2
Bowker	45°24′	72°14′	2.38	8.0	2.6±0.3
Champlain	44°44′	73°24′	1050	5.0	2.6±0.4
Libby	45°16′	72°22′	0.4	1.5	7.6±0.2
Lovering	45°11′	72°10′	4.2	4.8	3.2±0.7
Davignon	45°12′	72°44′	1.0	2.3	9.4±1.5
Boivin	45°42′	72°43′	2.2	0.9	13.5±16.3
Magog	45°17′	72°16′	10.5	2.3	12.0±3.6
Memphremagog (South Bay)	44°45′	72°12′	2.1	1.5	14.0±0.7
Memphremagog (Quinn Bay)	45°06′	72°15′	93.5	5.7	5.3±0.7

is available to the phytoplankton and can support their growth (Kuenzler and Perras 1965; Berman 1970; Aaronson and Patni 1976). A variety of enzymes capable of hydrolyzing organic phosphorus compounds are found in the freshwater plankton (Cembella et al. 1984a, 1984b). However, there is little definitive evidence indicating how, or to what extent, DOP is utilized by natural phytoplankton communities. The most often cited means by which the plankton are thought to acquire phosphorus from DOP is the cell surface enzyme alkaline phosphatase. Alkaline phosphatase is widespread among freshwater organisms (Jones 1972; Currie and Kalff 1984a). It is capable of hydrolyzing a great variety of phosphomonoesters (Herbes 1974), and its activity in the plankton has been shown to be related to the severity of phosphorus-deficiency (Kuenzler and Perras 1965; Healey and Hendzel 1975). Obviously, if one hypothesizes that phytoplankton might obtain phosphorus from DOP via alkaline phosphatase, then the enzyme must be associated with algal cells, not bacterial cells. Phosphatase is produced by both bacteria and algae (Jones 1972; Currie and Kalff 1984a), and Jones (1972) found that its activity in situ correlated with both algal and bacterial numbers. On the other hand, Berman (1970) and Pettersson (1980) suggested that phosphatase activity is predominantly algal, whereas Stewart and Wetzel (1982) and Wetzel (1981) reported that most phosphatase was either free in solution or associated with bacteria. If phosphatase were not generally found to be bound to phytoplankton cells, we could reject it as a potential supplier of phosphorus to the algae.

The purpose of our study was to test two specific hypotheses in a number of lakes: (1) that bacterioplankton are primarily responsible for orthophosphate uptake in situ, and (2) that alkaline phosphatase activity in situ is primarily associated with the phytoplankton. We tested these hypotheses by size-fractionating alkaline phosphatase activity and orthophosphate uptake in natural plankton communities, and by assessing the algal and bacterial contributions in each fraction.

Methods

We carried out size-fractionation experiments at 13 lake sites in the region of the Quebec – Vermont – New York borders. Study sites were chosen in an effort to sample a broad range of trophic conditions (Table 1). Each site was sampled once (with one exception) between 6 July and 26 August 1983. We have also included in our analyses, whenever possible, data from 11 visits to a single site (Lake Memphremagog, Quinn Bay) between 25 May and 1 October (Currie and Kalff 1984b).

At each site, we used a length of 2.5-cm Tygon tubing to draw an integrated epilimnetic water sample (to a maximum depth of 5 m). Secchi depth was noted at the same time. Water samples were immediately returned to our laboratory at Lake Memphremagog and analyses were begun. The uptake of orthophosphate by the plankton was partitioned into two size classes: uptake by particles retained on a 0.2-μm pore-diameter Nuclepore filter, and uptake by particles retained on a 3.0-μm filter. Alkaline phosphatase activities in the same size fractions were assayed. Finally, the partitioning of algae and bacteria between these two classes was assessed by size-fractionating indices of algal and bacterial activity: chlorophyll *a* and [^{14}C]bicarbonate uptake in the light as indicators of algal activity, and uptake of [^{14}C]glucose in the dark, indicating bacterial activity.

Orthophosphate uptake was partitioned as follows. Triplicate 50-mL subsamples of the integrated lake water were inoculated with carrier-free [^{32}P]orthophosphate (New England Nuclear). The subsamples were rapidly agitated, and 2.0-mL aliquots were withdrawn and filtered simultaneously through parallel 0.2- and 3.0-μm Nucleopore polycarbonate filters. This process was repeated at 0.5, 1, 2, 4, 8, 16, 30, and 60 min after inoculation with the isotope. The isotope activity retained on the filters was then determined by liquid scintillation counting in a high-efficiency fluor (Aquasol, New England Nuclear). The results were expressed as the percent of the total isotope activity retained on the filters as a function of time. For each size fraction, the initial slope of this function was estimated by fitting a second-degree polynomial to the data by least squares regression, and evaluating the first derivate at time zero (Currie and Kalff 1984a). This slope is equal to the rate constant of orthophosphate uptake. Since all the isotope is in solution in the form of orthophosphate at time zero, the estimated constant should be unaffected by any uptake or release of organic phosphorus.

TABLE 2. Portion of chlorophyll *a*, [^{14}C]glucose uptake, and $H^{14}CO_3^-$ uptake into particles larger than 3.0 μm, and the specific rate of orthophosphate uptake (in units of $10^{-3} \cdot min^{-1}$) and the alkaline phosphatase activity (in units of ng 3-*o*-methyl-fluorescein-phosphate hydrolysed $\cdot h^{-1} \cdot mL^{-1}$) of the whole plankton community (±95% C.I.) (*missing data).

Lake	Glucose >3.0 μm (%)	HCO_3^- >3.0 μm (%)	Chl *a* >3.0 μm (%)	PO_4 uptake >0.2 μm	PO_4 uptake >3.0 μm	Alkaline phophatase activity
Brome	21.1±11.8	75.2±18.3	91.3±1.6	23.8±6.2	5.03±1.01	11.4±6.0
Massawippi	6.8±3.8	93.7±22.7	80.1±4.7	150.±17.	16.4±2.6	27.6±13.3
Orford	17.4±5.7	79.5±15.9	62.9±10.4	106.±18.	12.7±2.6	25.1±9.3
Waterloo	70.5±11.0	105±23.9	91.4±1.8	81.9±13.1	53.3±6.1	76.9±51.6
Bowker	47.3±19.0	72.1±3.9	62.7±13.0	140.±67.	29.1±14.3	15.6±7.0
Champlain	11.2±3.9	65.2±13.3	78.2±5.8	56.1±47.3	2.39±1.00	13.7±5.4
Libby	38.3±4.9	84.3±14.3	74.9±5.1	220.±48.	56.8±19.0	33.5±14.3
Lovering	12.5±9.4	75.1±7.1	67.7±8.6	163.±26.	21.5±4.2	19.8±6.7
Davignon	30.2±7.3	82.9±14.2	63.2±15.6	140.±24.	32.1±4.8	21.8±4.9
Boivin	54.0±8.9	101±4.7	*	6.59±1.02	5.23±4.29	3.6±2.7
Magog	13.5±2.9	94.6±8.6	77.0±7.0	0.619±0.147	0.398±0.242	1.0±0.6
Memphremagog (South Bay)	*	73.1±5.6	79.8±6.1	89.8±17.5	23.8±3.8	31.5±9.2
Memphremagog (Quinn Bay, June 1983)	10.5±8.9	44.0±17.4	66.7±6.7	45.0±58.6	6.32±2.63	20.0±4.7
Memphremagog (Quinn Bay, July 1983)	12.9±4.5	97.9±19.7	80.9±17.2	82.7±15.1	3.94±0.84	17.1±4.1

The alkaline phosphatase activity associated with the various size fractions was assayed by preparing three treatments: whole, unmodified lakewater; lakewater that had been gently passed through a washed 3.0-μm Nucleopore filter; and finally a 0.2-μm filtrate. The enzyme activity in each treatment was then assayed using 3-*o*-methyl-fluorescein-phosphate as substrate. The fluorometer specifications and calibration are given by Smith and Kalff (1981). The activity associated with particles larger than 3.0 μm was found from the difference between the activity of whole lake water and that of the 3.0-μm filtrate. The activity of the fraction larger than 0.2 μm was estimated analogously. The enzyme activity in the 0.2-μm filtrate was regarded as soluble.

Partitioning of algae and bacteria between the two size fractions was assessed by size-fractionating indicators of algal and bacterial activity: chlorophyll *a* and [^{14}C]bicarbonate uptake in the light, and [^{14}C]glucose uptake in the dark (bacteria). The procedures used were similar to those used to separate orthophosphate uptake and alkaline phosphatase activity: isotope was incubated in lake water subsamples, and aliquots were filtered on 0.2- and 3.0-μm Nucleopore filters. The details and assumptions are discussed by Currie and Kalff (1984b).

Based on the distribution of these physiological indicators between size fractions, one may estimate how much of the orthophosphate uptake and phosphatase activity are due to phytoplankton versus bacterioplankton. To do this, we assume that the uptake of trace quantities of [^{14}C]glucose in the dark is entirely bacterial and that uptake of [^{14}C]bicarbonate in the light (dark bottle corrected) is entirely algal. Neither assumption is strictly true, but departures from them and the errors therein entailed are probably very small (cf. Wright and Hobbie 1966; Berman and Stiller 1977; Bonin and Maestrini 1981). We further assume that bacterial orthophosphate uptake is distributed between the two size fractions in the same proportion as is bacterial glucose uptake and that algal orthophosphate uptake is distributed as is algal bicarbonate uptake. Based upon these assumptions, one can write a pair of simultaneous equations describing the portions of algal and bacterial uptake on each filter type. The equations can then be solved explicitly for algal uptake and bacterial uptake. Violations of the assumptions, although probably not extreme, tend to overestimate the importance of algae (Currie and Kalff 1984b). The results of this calculation are rather imprecise if one propagates the numerous error terms, but they should nonetheless provide unbiased approximations of the relative amounts of algal and bacterial activity.

The precision of individual measurements in this study was usually good: most coefficients of variation of direct measurements were on the order of 5−10%. In most cases, the final results were functions of these basic statistics (e.g. the ratios of two variables). The variances of arithmetic functions of the basic statistics were estimated by Taylor approximations, as discussed by Colquhoun (1971, section 2.7). Resulting variance estimates appear large (e.g. Fig. 1 and 7) because they are very conservative (D. J. Currie, unpubl. data).

Results

We present our results in terms of orthophosphate and alkaline phosphatase partitioning between size fractions (smaller than 3 μm and larger than 3 μm), as well as between algae and bacteria. We do this for statistical reasons. The 3.0-μm division was chosen somewhat arbitrarily in an effort to separate algae and bacteria (cf. Berman and Stiller 1977; Currie and Kalff 1984b). The separation was imperfect, as may be judged by the extent to which chlorophyll and bicarbonate uptake are associated with particles smaller than 3.0 μm, and the tendency for glucose uptake to be larger than 3.0 μm (Table 2). However, the fraction larger than 3.0 μm includes most of the phytoplankton (63−91% of the chlorophyll is in this fraction), and its phosphatase activity and orthophosphate uptake can be estimated precisely. The explicit estimates of algal and bacterial activity are less precise, but more biologically interesting.

Uptake of Orthophosphate

How does orthophosphate size partitioning vary among lakes? We posed this question because, in single lake studies,

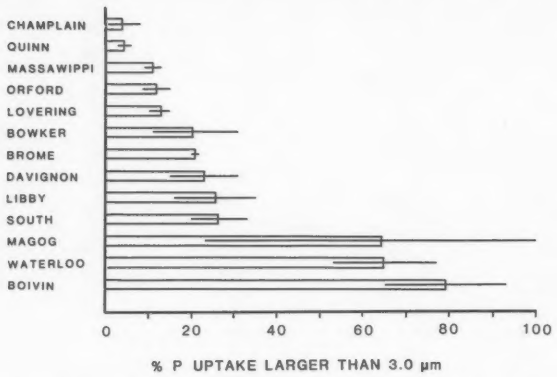


FIG. 1. Portion of orthophosphate uptake into particles larger than 3.0 µm in 13 lakes. Bars represent 95% confidence limits.

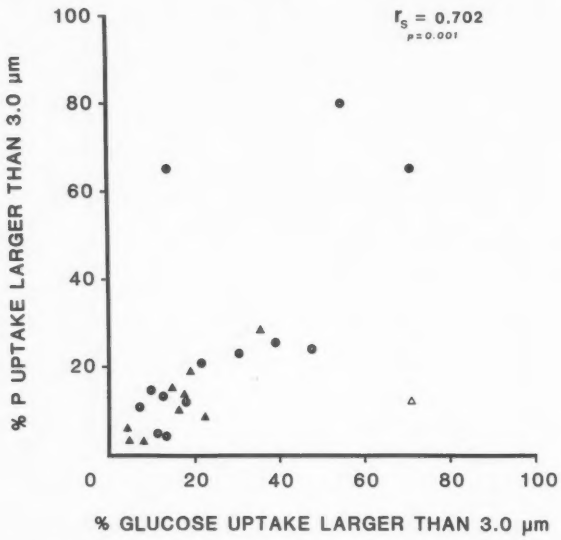


FIG. 2. Relationship between the percentage of glucose uptake larger than 3.0 µm and the percentage of orthophosphate uptake larger than 3.0 µm. ●, data from this study; ▲, data from Currie and Kalff (1984b). The coefficient of variation of point △ is an order of magnitude larger than those of other observations.

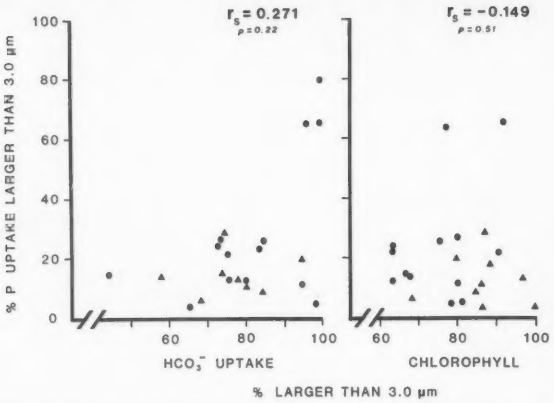


FIG. 3. Relationship between the percentage of orthophosphate uptake larger than 3.0 µm and the percentage of [^{14}C]bicarbonate uptake (left) or chlorophyll (right) larger than 3.0 µm. ●, data from this study; ▲, data from Currie and Kalff (1984b).

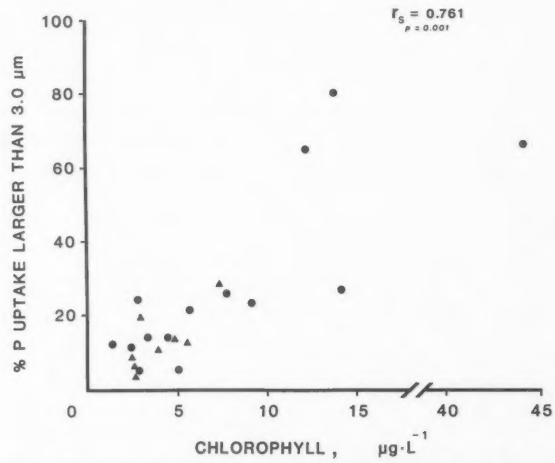


FIG. 4. Relationship between chlorophyll concentration and the percentage of the total community orthophosphate uptake associated with particles larger than 3.0 µm. ●, data from this study; ▲, data from Currie and Kalff (1984b).

most authors have observed that the smallest planktonic particles are preponderantly responsible for orthophosphate uptake (e.g. Rigler 1956; Currie and Kalff 1984b), yet there is at least one diametrically opposed exception (Lake Michigan; R. Moll and S. J. Tarapchak, unpubl. data). In this study, we found that >73% of the uptake was into particles smaller than 3.0 µm in 10 of 13 lakes (Fig. 1). Similarly, in Lake Memphremagog, the proportion of orthophosphate uptake smaller than 3.0 µm varied between 97% in late spring and 71% in early autumn (Currie and Kalff 1984b). However, in the remaining three lakes (Waterloo, Boivin, and Magog), 65−80% of the uptake was into particles larger than 3.0 µm. Orthophosphate uptake is obviously not invariably dominated by small particles.

What accounts for this variation? Several points emerge from our analysis. First, the partitioning of orthophosphate uptake between size fractions is strongly correlated with the partitioning of glucose uptake between those size fractions (Fig. 2; Spearman's $r_s = 0.702$, $P = 0.001$, $n = 23$). That is, when more of the bacteria are associated with large particles, more of the orthophosphate uptake is also in that fraction. Conversely, it is not correlated with the partitioning of bicarbonate uptake ($r_s = 0.272$, $P = 0.22$, $n = 22$) or chlorophyll ($r_s = 0.148$, $P = 0.51$, $n = 22$) between the two size fractions (Fig. 3). In other words, the distribution of algae among size fractions is not related to the distribution of orthophosphate uptake. These observations are consistent with the hypothesis that orthophosphate uptake is largely a function of bacterial activity and not algal.

Second, the percentage of orthophosphate uptake by particles larger than 3.0 µm was postively related to the total amount of chlorophyll present (Fig. 4; Spearman's $r_s = 0.761$, $P = 0.001$, $n = 22$) and negatively related to the Secchi depth

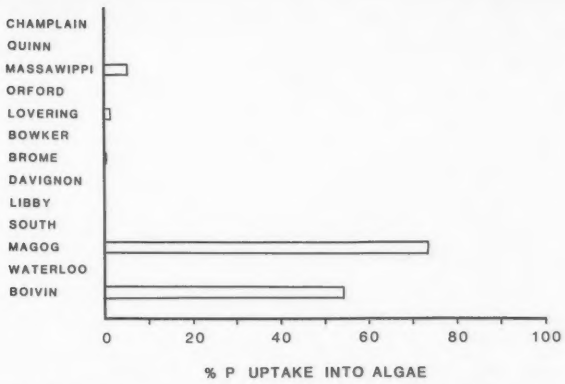


FIG. 5. Estimated share of the total community uptake of orthophosphate that is due to phytoplankton activity. The absence of a bar indicates that phytoplankton were estimated to be responsible for ≤0% of the orthophosphate uptake.

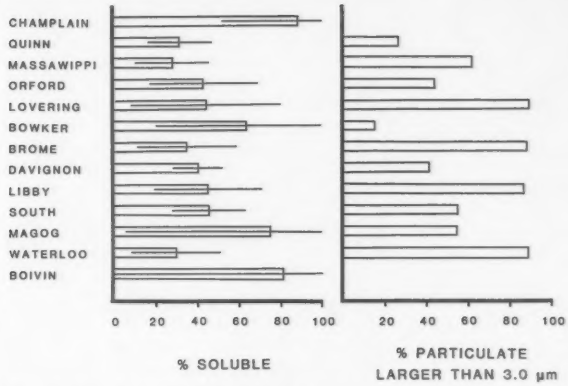


FIG. 6. Size distribution of alkaline phosphatase activity. The percentage of activity in solution is shown to the left, and the percentage of the remaining particulate activity that is larger than 3.0 μm is given to the right. Bars represent 95% confidence intervals.

($r_s = -0.767$, $P = 0.03$, $n = 13$). The seasonal variation in orthophosphate uptake partitioning in Quinn Bay, Lake Memphremagog, was indistinguishable from this pattern (Fig. 2). In other words, the greater the plankton biomass, the greater the portion of orthophosphate uptake into large particles. Third, the partitioning is negatively correlated with the size of the lake ($r_s = -0.589$, $P = 0.035$, $n = 13$). We suggest that this is probably due to an even stronger negative correlation between the absolute amount of uptake in larger particles and lake size ($r_s = -0.724$, $P = 0.006$, $n = 13$). Finally, orthophosphate partitioning is very strongly correlated with two measures of phosphorus deficiency: the total alkaline phosphatase activity per unit chlorophyll ($r_s = -0.727$, $P = 0.004$, $n = 14$), and the phosphorus turnover time per unit chlorophyll ($r_s = 0.502$, $P = 0.018$, $n = 22$). However, these two correlations may be trivial: the first because partitioning is also correlated with chlorophyll alone ($r_s = 0.761$, $P = 0.001$, $n = 22$), and the second because it is a part–whole correlation.

The relative contributions of phyto- and bacterioplankton in this process may be estimated as we described. Currie and Kalff (1984b) found that >96% of the orthophosphate uptake in Quinn Bay was bacterial at any given moment during the ice-free season. In the present study, we found that >95% of the orthophosphate uptake was estimated to be bacterial in all but two of the lakes examined (Fig. 5). Indeed, in many cases the algal contribution to orthophosphate uptake was apparently nil. In the two clear exceptions, Lakes Magog and Boivin, more than half of the uptake was estimated to be algal. One ambiguous case was Lake Waterloo, where 65% of the orthophosphate uptake was larger than 3.0 μm, but the phytoplankton were estimated to take up an insignificant amount of the orthophosphate. This is because most of the bacterial activity was also larger than 3.0 μm, presumably due to bacterial attachment to particles. In cases of very poor size separation, such as Waterloo, the assumptions involved in separating algal and bacterial activity appear more tenuous, and the resulting calculation is, therefore, more likely to be in error. In sum, bacteria are responsible for nearly all the orthophosphate uptake in many lakes, but there are evident exceptions.

It might be argued that orthophosphate uptake by small particles could be due to pico-phytoplankton, and not to bacteria. Picoplankton have been observed in the lakes we studied (D. F. Bird, McGill University, pers. comm.) and, on the basis of cell size, one would expect them to be reasonably effective competitors for phosphorus (Currie and Kalff 1984a). However, we have used bicarbonate uptake as the indicator of algal activity in each size fraction. Since the smallest algal cells take up bicarbonate, again as a function of cell size (Banse 1976; Gutelmacher and Petrova 1983), we have controlled for the presence of picoplankton in the smallest size fraction. The conclusion that bacterioplankton took up most of the phosphorus is still valid, but it seems likely that the small portion that goes to phytoplankton is predominantly taken up by picoplankton.

Alkaline Phosphatase Activity

Alkaline phosphatase activity is related to the severity of phosphorus deficiency in lakes (Fitzgerald 1969; Berman 1970; Sproule and Kalff 1978; Pettersson 1980). In our data set, we observed considerable variation among lakes in the total phosphatase activity (Table 2). It correlated positively ($r_s = 0.627$, $P = 0.017$, $n = 14$) with the rate constant of orthophosphate uptake by the entire community (i.e. particles larger than 0.2 μm), a parameter that is very close to the orthophosphate turnover rate. This indicates that phosphatase is most abundant in systems with the highest phosphorus demand. The alkaline phosphatase activity is even more strongly related to the rate constant of uptake into particles larger than 3.0 μm ($r_s = 0.763$, $P = 0.002$, $n = 14$) (i.e. primarily the phytoplankton).

Our reason for investigating alkaline phosphatase was to determine whether the activity is primarily algal or bacterial. The size-fractionation of alkaline phosphatase was very different from that of orthophosphate uptake (Fig. 6). First, much of the phosphatase was free in solution (31–87%, median 44%). Considering the particulate portion of phosphatase only, we again observed considerable variability in the fraction associated with particles larger than 3.0 μm (0–89%). This variable was not statistically related to any of the other variables we observed, perhaps due to poor precision. It is nearly significantly correlated with the portion of chlorophyll larger than 3.0 μm ($r_s = 0.506$, $P = 0.078$, $n = 13$), but is entirely unrelated to the partitioning of glucose uptake ($r_s = 0.030$, $P < 0.5$, $n = 13$). It is important to note that the share of

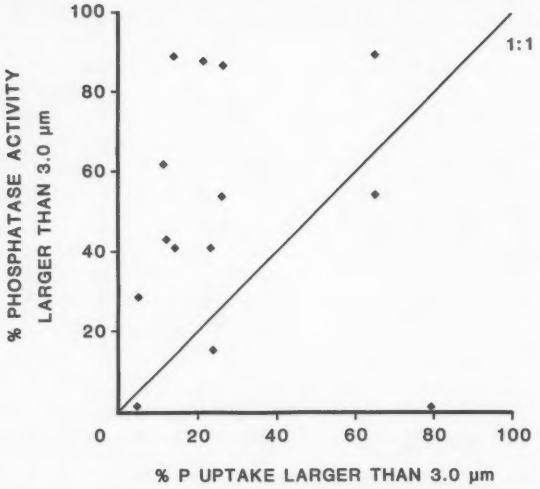


FIG. 7. Relationship between the percentage of orthophosphate uptake associated with particles larger than 3.0 µm and the percentage of alkaline phosphorus activity larger than 3.0 µm.

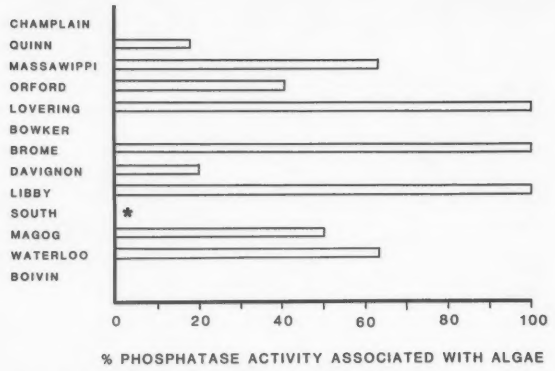


FIG. 8. Estimated percentage of the particulate alkaline phosphatase activity that is associated with algae. * Insufficient data.

phosphatase activity associated with the larger particles in all lakes was nearly always much greater than the share of orthophosphate uptake in larger particles (Fig. 7). We estimate that the algae were responsible for much of the particulate phosphatase activity in most lakes (Fig. 8).

Discussion

Our first purpose in this study was to determine if bacterioplankton are primarily responsible for orthophosphate uptake in a wide variety of systems. In the lakes we examined, they were predominant in most systems, but not all. We now propose two more general hypotheses: that the partitioning of orthophosphate uptake between algae and bacteria depends upon lake trophic status and upon phosphorus deficiency.

Our data support both these hypotheses. First, lakes with more chlorophyll have more uptake into the larger particles (Fig. 2). Chlorophyll concentration is indicative not only of algal biomass, it is also well correlated with the biomass of bacteria (Bird and Kalff 1984), zooplankton (McCauley and Kalff 1981), and other organisms. We infer that Fig. 2 is consistent with a relationship between trophic status and orthophosphate partitioning.

Second, orthophosphate uptake by algae is greatest in the least phosphorus-deficient lakes. This hypothesis is supported by the correlations we found between uptake partitioning and the indices of phosphorus deficiency cited above. The two lakes in which we observed significant amounts of algal uptake of orthophosphate — Magog and Boivin — are apparently the two least phosphorus-deficient lakes we sampled. They had the lowest alkaline phosphatase activities and the slowest orthophosphate uptake constants of all the lakes in our study, despite their high chlorophyll concentrations. Both lakes also receive considerable loadings of urban sewage. These observations appear to be analogous to the results of Lean and White (1983), who observed that larger particles in lake water are responsible for a greater portion of the orthophosphate uptake when additional unlabelled orthophosphate is added to the water. Bacterial uptake systems saturate at much lower orthophosphate concentrations than do algal systems (Currie and Kalff 1984a). As a result, when higher concentrations of orthophosphate are present, one would expect a higher proportion of algal uptake. We conclude that algae are capable of effectively competing for orthophosphate only when orthophosphate is plentiful.

Evidence from other published studies also supports the hypothesis that algal–bacterial phosphorus partitioning is dependent upon the severity of phosphorus limitation. In a study identical in design to the present work, Berman (1985) examined the seasonal variation in orthophosphate uptake in Lake Kinneret. He concluded that bacteria were responsible for much of the uptake of orthophosphate, but that the phytoplankton did compete with some success. Reexamining the data Berman presents, we find patterns in Lake Kinneret that are very similar to those we found. In Kinneret, the seasonal variation in the size distribution of orthophosphate uptake is related to the distribution of glucose uptake (i.e. bacteria) between size fractions (Spearman's $r_s = 0.542$, $P = 0.021$, $n = 15$) but is not significantly related to the distribution of bicarbonate uptake ($r_s = 0.291$, $P > 0.2$, $n = 12$) nor to the chlorophyll distribution ($r_s = 0.242$, $P > 0.2$, $n = 15$) (i.e. algae). Again similarly to our findings, the orthophosphate partitioning covaries with orthophosphate turnover time ($r_s = 0.559$, $P = 0.014$, $n = 16$). However, it does not covary with the total chlorophyll concentration (which varied about as much in Lake Kinneret as in our data set) ($r_s = 0.068$, $P > 0.5$, $n = 15$). Estimating the relative algal and bacterial contributions to the total community uptake, bacteria are again responsible for the vast majority, except when orthophosphate uptake was very slow ($<0.004 \cdot \text{min}^{-1}$; cf. Boivin and Magog, Table 2). These results support the hypothesis that orthophosphate uptake partitioning between algae and bacteria is principally a function of the severity of phosphorus deficiency.

In other published studies we find similar evidence. In lakes with rapid orthophosphate turnover, the smallest particles in the plankton take up most of the orthophosphate (Rigler 1956; Burnison 1975; Koschel 1980; Lean and White 1983), whereas in slow turnover lakes, more uptake is associated with larger particles (Koschel 1980). In Koschel's (1980) data from eight East German lakes, we observe that the portion of orthophosphate uptake in the smallest size class (<1.5 µm) is strongly related to the orthophosphate turnover time ($r_s = -0.838$, $P = 0.007$, $n = 8$), but not to the qualitative description of

trophy ($r_s = 0.327$, $P < 0.1$, $n = 8$). Therefore, the hypothesis supported most broadly by our work and our interpretation of the results of others is that orthophosphate uptake in lakes is largely or entirely bacterial, except where the community phosphate demand (as evidenced by the orthophosphate turnover rate) is low.

Two studies are clearly at variance with this hypothesis. Paerl and Lean (1976) reported algae to be the prime pathway of orthophosphate uptake in Heart Lake (Ontario, Canada), although they did not explicitly show this. At the time of their experiments, biomass was high (40 μg Chl $a \cdot L^{-1}$) and orthophosphate turnover was rapid ($0.2 \cdot min^{-1}$). R. Moll and S. J. Tarapchak (unpubl. data), based upon more explicit tests, reached the same conclusion for Lake Michigan (Chl *a*: 0.2 − 2.4 $\mu g \cdot L^{-1}$; turnover; $0.005 - 0.17 \cdot min^{-1}$). Possibly, methodological differences are responsible for this discrepancy, since these two studies alone employed different techniques. Or, our hypothesis may be incorrect. At present, we note only that our hypothesis is consistent with observations from 25 lakes (Rigler 1956; Burnison 1975; Koschel 1980; Lean and White 1983; Berman 1985; present study) and is inconsistent with two (Paerl and Lean 1976; Moll and S. J. Tarapchak, unpubl. data) (sign test, $P < 0.0001$, $n = 27$).

The second goal of this study was to determine if we could reject alkaline phosphatase-hydrolyzed organic phosphorus compounds as a potential source of phosphorus for the phytoplankton. Unfortunately, our results are not entirely unequivocal. Much of the alkaline phosphatase in the lakes we studied was free in solution. This phenomenon was also observed by Stewart and Wetzel (1982). They concluded that free phosphatase activity did not represent a procedural artifact, since similar patterns were observed in gentler centrifugation studies. The free phosphatase is likely to be a mixture of zooplankton digestive phosphatases (Jannson 1976; Boavida and Heath 1984) and algal and/or bacterial enzymes, released passively or as a result of grazing. The action of free phosphatase would tend to liberate orthophosphate into solution. Our results above indicate that this would ordinarily be primarily available to bacterioplankton. Therefore, soluble alkaline phosphatase would not provide phosphorus to the phytoplankton.

The particulate portion of phosphatase activity was divided between algae and bacteria in a manner that varied widely among lakes. In general, our data indicate that algae are responsible for more of the alkaline phosphatase activity than they are for orthophosphate uptake. There are also indications that phosphatase activity in situ may be somewhat better related to phytoplankton activity than to bacterial (see Results). Our results cannot reject phosphatase-derived phosphorus as a significant source of phosphorus for the phytoplankton, but neither can they lend this hypothesis more than weak support.

Our results leave at least two intriguing problems unsolved: whence the algae get their phosphorus, and how to interpret the large portion of phosphorus that the bacteria get. An appealing possibility is that bacteria may recycle phosphorus much more rapidly than algae (cf. Berman and Skyring 1979). However, there is no extant evidence of such an imbalance (Currie and Kalff 1984b, 1984c). Our data do not exclude the possibility that algae do get their phosphorus from orthophosphate — they are usually responsible for some finite fraction of the uptake — but the quantities involved are extremely small (D. J. Currie, unpubl. data). The poor ability of algae to compete for inorganic phosphorus suggests that they may instead use organic phosphorus, but the evidence for this hypothesis is inconclusive (cf. Taft et al. 1977; Currie and Kalff 1984b; Berman 1985; present study). Perhaps bacteria dominate phosphorus (as well as orthophosphate) uptake most of the time in many lakes. If this is true, then the textbook paradigm of phosphorus cycling in lakes and the ubiquitous models of orthophosphate-dependent phytoplankton growth are wrong.

Acknowledgements

We are much indebted to L. Rath, S. J. Tarapchak, and two anonymous reviewers for their thoughtful criticisms of earlier drafts of this manuscript. We are also grateful to M. R. Anderson and Y. Prairie for their assistance with the field work, and to A. Hilton for preparing the manuscript. Funding was provided by grants from the Natural Sciences and Engineering Research Council of Canada to Dr. J. Kalff. Personal support to D.C. was provided by the Fonds F.C.A.C. of the Ministère de l'Education du Québec.

References

AARONSON, S., AND N. J. PATNI. 1976. The role of surface and extracellular phosphatase in the phosphorus requirement of *Ochromonas*. Limnol. Oceanogr. 21: 838–845.

BANSE, K. 1976. Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size — A review. J. Phycol. 12: 135–140.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 24: 541–547.

1985. Uptake of ^{32}P-orthophosphate by algae and bacteria in Lake Kinneret. J. Plankton Res. 7: 71–84.

BERMAN, T., AND G. W. SKYRING. 1979. Phosphorus cycling in aquatic microorganisms studied by phased uptake of ^{33}P and ^{32}P. Curr. Microbiol. 2: 47–49.

BERMAN, T., AND M. STILLER. 1977. Simultaneous measurement of phosphorus and carbon uptake in Lake Kinneret by multiple isotopic labeling and differential filtration. Microb. Ecol. 3: 279–288.

BIRD, D. F., AND J. KALFF. 1984. Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. Can. J. Fish. Aquat. Sci. 41: 1015–1023.

BOAVIDA, M. J., AND R. T. HEATH. 1984. Are the phosphatases released by *Daphnia magna* components of its food? Limnol. Oceanogr. 29: 641–645.

BONIN, D. J., AND S. Y. MAESTRINI. 1981. Importance of organic nutrients for phytoplankton growth in natural environments: implications for algal species succession. *In* T. Platt [ed.] Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210. 279–291.

BURNISON, K. B. 1975. Microbial ATP studies. Verh. Int. Ver. Limnol. 19: 286–290.

CEMBALLA, A. D., N. J. ANTIA, AND P. J. HARRISON. 1984a. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective: Part I. CRC Crit. Rev. Microbiol. 10: 317–391.

1984b. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective: Part II. CRC Crit. Rev. Microbiol. 11: 13–81.

COLQUHOUN, D. 1971. Lectures in biostatistics. Clarendon Press, Oxford. 425 p.

CURRIE, D. J., AND J. KALFF. 1984a. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. Limnol. Oceanogr. 29: 298–310.

1984b. The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in fresh water. Limnol. Oceanogr. 29: 311–321.

1984c. Can bacteria outcompete phytoplankton for phosphorus? A chemostat test. Microb. Ecol. 10: 205–216.

FITZGERALD, G. P. 1969. Field and laboratory evaluations of bioassays for nitrogen and phosphorus with algae and aquatic weeds. Limnol. Oceanogr. 14: 206–212.

GOLDMAN, C. R., AND A. J. HORNE. 1983. Limnology. McGraw-Hill, New York, NY.

GUTELMACHER, B. L., AND N. A. PETROVA. 1983. Production of individual species of algae and its role in the productivity of phytoplankton in Lake Ladoga. Int. Rev. Gesamten Hydrobiol. 67: 613–624.

HAYES, F. R., AND J. E. PHILLIPS. 1958. Lake water and sediment. IV. Radiophosphorus equilibrium with mud, plants and bacteria under oxidized and reduced conditions. Limnol. Oceanogr. 3: 459–475.

HEALEY, F. P., AND L. L. HENDZEL. 1975. Effect of phosphorus deficiency on two algae growing in chemostats. J. Phycol. 11: 303–309.

HERBES, S. 1974. Biological utilizability of dissolved organic phosphorus in natural waters. Ph.D. thesis, University of Michigan, Ann Arbor, MI. 236 p.

JANNSON, M. 1976. Phosphatases in lakewater. Characterization of enzymes from phytoplankton and zooplankton by gel filtration. Science (Wash., DC) 194: 320–321.

JONES, J. G. 1972. Studies on freshwater bacteria: association with algae and alkaline phosphatase activity. J. Ecol. 60: 59–75.

KALFF, J., AND R. KNOECHEL. 1978. Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. Annu. Rev. Ecol. Syst. 9: 475–495.

KOSCHEL, R. 1980. Untersuchungen zur Phosphataffinität des Planktons in der euphotischen Zone von Seen. Limnologica (Berlin) 12: 141–145.

KUENZLER, E. J., AND J. P. PERRAS. 1965. Phosphatases of marine algae. Biol. Bull. (Woods Hole) 128: 271–284.

LEAN, D. R. S., AND E. WHITE. 1983. Chemical and radiotracer measurements of phosphorus uptake by lake plankton. Can. J. Fish. Aquat. Sci. 40: 147–155.

MCCAULEY, E., AND J. KALFF. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Can. J. Fish. Aquat. Sci. 38: 458–463.

NALEWAJKO, C., AND D. R. S. LEAN. 1980. Phosphorus, p. 235–258. *In* I. Morris [ed.] The physiological ecology of phytoplankton. University of California Press, Berkeley, CA.

PAERL, H. W., AND D. R. S. LEAN. 1976. Visual observations of phosphorus movement between algae, bacteria, and abiotic particles in lake waters. J. Fish. Res. Board Can. 33: 2805–2813.

PETTERSSON, K. 1980. Alkaline phosphatase and algal surplus phosphorus as a phosphorus-deficiency indicator in Lake Erken. Arch. Hydrobiol. 89: 54–87.

RIGLER, F. H. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37: 550–562.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

SMITH, R. E. H., AND J. KALFF. 1981. The effect of phosphorus limitation on algal growth rates: evidence from alkaline phosphatase. Can. J. Fish. Aquat. Sci. 38: 1421–1427.

SPROULE, J. L., AND J. KALFF. 1978. Seasonal cycles in the phytoplankton phosphorus status of a north temperate zone lake (Lake Memphremagog, Qué-Vt) plus a comparison of techniques. Verh. Int. Ver. Limnol. 20: 2681–2688.

STEWART, A. J., AND R. G. WETZEL. 1982. Phytoplankton contribution to alkaline phosphatase activity. Arch. Hydrobiol. 93: 265–271.

TAFT, J. L., M. E. LOFTUS, AND W. R. TAYLOR. 1977. Phosphate uptake from phosphomonesters by phytoplankton in the Chesapeake Bay. Limnol. Oceanogr. 22: 1012–1021.

TILMAN, D. 1977. Resource competition between plankton algae in an experimental and theoretical approach. Ecology 58: 338–348.

WETZEL, R. G. 1981. Longterm dissolved and particulate alkaline phosphatase activity in a hardwater lake in relation to lake stability and phosphorus enrichments. Verh. Int. Ver. Limnol. 21: 369–381.

1983. Limnology. 2nd ed. W. B. Saunders Co., Philadelphia, PA. 767 p.

WRIGHT, R. T., AND J. E. HOBBIE. 1966. Use of glucose and acetate by bacteria and algae in aquatic ecosystems. Ecology 47: 447–464.

Phosphate Uptake by Microorganisms in Lake Water: Deviations from Simple Michaelis–Menten Kinetics[1,2]

Stephen J. Tarapchak and Lynn R. Herche

Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, 2300 Washtenaw Avenue, Ann Arbor, MI 48104, U.S.A.

Tarapchak, S. J., and L. R. Herche. 1986. Phosphate uptake by microorganisms in lake water: deviations from simple Michaelis–Menten kinetics. Can. J. Fish. Aquat. Sci. 43: 319–328.

Orthophosphate ($^{31}P_i$) uptake rates by natural Lake Michigan microbial assemblages were measured to test a hypothesis that the instantaneous velocity of $^{31}P_i$ uptake at low added substrate concentrations is higher than predicted by the simple Michaelis–Menten equation. Analysis of data from most experiments verified this prediction: $^{31}P_i$ turnover times (T_{calc}) obtained by back-extrapolating from "low" substrate regions in Woolf plots ranged from 25% to nearly 3000% of those calculated from "high" substrate regions. Simulation analysis demonstrated that deviations in T_{calc} could be at least an order of magnitude higher than previously predicted. Large (>1000%) discrepancies from the simple Michaelis–Menten equation could be caused by "skewed" or "clumped" distributions, where the range in both species half-saturation constants (K_t) and relative abundances is very wide and species with the lowest K_t values are most abundant. A comparison of K_t values for mixed microbial assemblages in Lake Michigan (0.16–19.4 μg $P \cdot L^{-1}$) with those from laboratory culture studies (11–364 μg $P \cdot L^{-1}$) demonstrates that natural microbial populations have adapted to P-limited environments by synthesizing uptake systems that have K_t values at least an order of magnitude below those detected in culture studies.

La vitesse d'absorption de l'ortophosphate ($^{31}P_i$) par des assemblages microbiens naturels du lac Michigan a été déterminée dans le but de vérifier une hypothèse voulant que la vitesse instantanée de l'absorption du $^{31}P_i$ à de faibles concentrations de substrat soit plus élevée que celle prévue par l'équation simple de Michaelis–Menten. L'analyse des données de la plupart des essais a confirmé la prévision : les temps de renouvellement du $^{31}P_i$ (T_{calc}) obtenus par extrapolation inverse à partir des zones de « faibles » concentrations de substrat des tracés de Woolf variaient de 25 % à près de 3 000 % des valeurs calculées à partir des zones de « hautes » concentrations de substrat. L'analyse par simulation a montré que les écarts de T_{calc} pouvaient être supérieurs d'au moins un ordre de grandeur à ceux antérieurement prévus. Les écarts importants (>1 000 %) par rapport à l'équation simple de Michaelis–Menten pourraient avoir pour origine des distributions « asymétriques » ou « en grappes » où la gamme des constantes de demi-saturation des espèces (K_t) et des abondances relatives est très large et pour lesquelles les espèces à valeur de K_t les plus faibles sont les plus abondantes. La comparaison des valeurs K_t d'assemblages microbiens mixtes du lac Michigan (0,16–19,4 μg $P \cdot L^{-1}$) avec celles de cultures de laboratoire (11–364 μg $P \cdot L^{-1}$) a montré que les populations microbiennes naturelles se sont adaptées à des milieux pauvres en P en synthétisant des systèmes d'absorption à valeurs de K_t inférieures d'au moins un ordre de grandeur à celles des cultures.

Received September 14, 1984
Accepted September 6, 1985
(J7961)

Reçu le 14 septembre 1984
Accepté le 6 septembre 1985

Limnologists frequently study phosphorus–microbial dynamics by measuring the kinetics of orthophosphate ($^{31}P_i$) uptake by natural populations (e.g. Nalewajko et al. 1981; Lean and Pick 1981; Lehman and Sandgren 1982; Lean and White 1983). The velocity (v) of nutrient uptake versus substrate concentration is fitted to the Michaelis–Menten equation:

$$(1) \quad v = \frac{V_{max} \cdot S}{K_t + S}$$

where V_{max} is maximum v when uptake sites are saturated with $^{31}P_i$, K_t is the half-saturation constant (the $^{31}P_i$ concentration when v is one-half V_{max}) (cf. Wright and Hobbie 1966), and S is the sum ($\Sigma^{31}P_i$) of the added ($^{31}P_a$) and ambient ($^{31}P_n$) orthophosphate concentrations. Applying equation (1) to natural assemblages assumes that v for each species can be described by equation (1) and that v for all species combined approximates the simple Michaelis–Menten equation.

Simulation studies, however, show that at low substrate levels, assemblages composed of species with different K_t's take up limiting nutrients at greater rates than predicted by equation (1) (Williams 1973). This can be illustrated by plotting turnover time (T_{calc}) against substrate concentration (Fig. 1). The curve is linear at "high" concentration, but becomes nonlinear at lower concentrations, resulting in a faster T_{calc} (y-axis intercept) and a lower K_t (negative x-axis intercept) when back-extrapolated from points in the "low" substrate region. Williams (1973) showed that the error in estimating true

[1]This paper is partly based on a presentation at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

[2]GLERL Contribution No. 423.

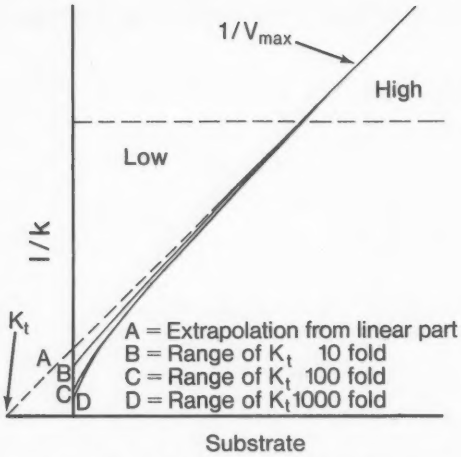


FIG. 1. Woolf plot of turnover time ($1/k$) versus substrate concentration illustrating simulated nonlinearity in the "low" substrate region caused by the presence of species populations with different K_t ranges and equal abundances (redrawn and relabeled from Williams 1973).

T_{calc} varies with the range in species K_t and the position of the assemblage K_t relative to ambient substrate concentration. For example, the deviation was highest (213%) when substrate concentration was low relative to assemblage K_t, when K_t ranged 1000-fold and values were uniformly distributed within each order of magnitude. Conversely, the error was negligible (<6%) when $^{31}P_n$ was greater than assemblage K_t. To estimate kinetic constants accurately, one must add limiting substrates at concentrations less than assemblage K_t and back-extrapolate from the near-linear part of the curve at "low" substrate levels (Williams 1973).

Despite the need for accurate estimates of kinetic constants in ecologic studies (e.g. Lean and Pick 1981; Lehman and Sandgren 1982), Williams' predictions have been tested for $^{31}P_i$ only once — an experiment on water from Lake Wingra, WI (Brown et al. 1978). Two a priori arguments suggest that the maximum deviation predicted by Williams should occur in P-limited oligotrophic and mesotrophic lakes. First, deviations should be independent of species number because these lakes are characterized by high diversity. Second, $^{31}P_n$ should be less than assemblage K_t. Epilimnetic $^{31}P_n$ concentrations are usually in the submicrogram per litre range (Rigler 1966; Levine and Schindler 1980; Tarapchak et al. 1982a), whereas assemblage K_t usually exceeds 5 $\mu g\ P \cdot L^{-1}$ (cf. Nalewajko and Lean 1980). We tested Williams' predictions for microbial $^{31}P_i$ uptake and performed simulation analysis to determine possible causes of deviations from the simple Michaelis–Menten equation.

Kinetic Analysis, Experimental Rationale, and Methodology

Analysis of Kinetic Data

Experiments are normally performed by spiking subsamples with unlabeled ($^{31}P_a$) and radiolabeled ($^{33}P_i$) orthophosphate, measuring the rate constant (k) for loss of $^{33}P_i$ from solution, and multiplying k by $\Sigma^{31}P_i$ to obtain the instantaneous $^{31}P_i$ uptake velocity (v) (e.g. Lean and Pick 1981). Traditionally, linear transformation is used to obtain uptake constants (e.g.

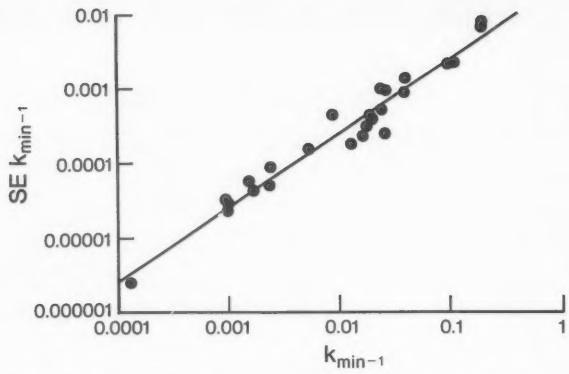


FIG. 2. Plot showing the error in estimating k as a function of k.

Dowd and Riggs 1965; Halmann and Stiller 1974; Lean and Pick 1981). In the most common transformation, the Woolf plot, v is eliminated from equation (1) by dividing by $\Sigma^{31}P_i$ to give the uptake rate coefficient, $k(h^{-1})$:

$$(2)\quad k = \frac{v}{\Sigma^{31}P_i} = \frac{V_{max}}{K_t + \Sigma^{31}P_i}$$

and the equation is inverted:

$$(3)\quad \frac{1}{k} = \frac{K_t}{V_{max}} + \frac{\Sigma^{31}P_i}{V_{max}}$$

When $1/k$ is plotted against $\Sigma^{31}P_i$, the reciprocal of the slope is V_{max}, the intercept of the negative x-axis is $-K_t$, and the intercept of the y-axis (K_t/V_{max}) equals the calculated turnover time (T_{calc}) of the $^{31}P_n$ pool when $\Sigma^{31}P_i = 0$ (Wright and Hobbie 1966). This transformation was used for direct comparisons with Williams' predictions.

To obtain kinetic constants, we used a least-squares optimization program for equation (3). The analysis was designed to generate a plot of $1/k$ versus $\Sigma^{31}P_i$ and a corresponding plot of residual values. The trend in residuals was used to identify the approximate $\Sigma^{31}P_i$ concentration where the $1/k$ versus $\Sigma^{31}P_i$ curve departs from linearity (Fig. 1). Once this point was established, data in the "high" (h) and "low" (l) substrate regions were fitted using weighted linear regression analysis and back-extrapolated to obtain T^h_{calc}, T^l_{calc}, K^h_t, and K^l_t, respectively. Percentage differences between T_{calc} (computed by subtracting T^l_{calc} from T^h_{calc} and dividing by T^l_{calc}) were evaluated by applying a two-sample t-test (Brownlee 1965) using variance estimates from an error analysis of $1/k$ (Fig. 2) (see Experimental Design). Difference between K_t's was calculated in the same way. Plots of predicted v versus $\Sigma^{31}P_i$, based on constants from "high" and "low" substrate regions, were generated to contrast differences in uptake at ambient $^{31}P_n$.

Experimental Design

Williams' (1973) prediction can only be tested experimentally if five conditions are satisfied: (1) steady state must hold during incubation, (2) the lowest $^{31}P_a$ must be less than assemblage K_t, (3) equation (3) must provide statistically accurate estimates of kinetic constants, (4) estimates of $^{31}P_n$ must be accurate or limited in their potential range, and (5) experimental errors must be negligible. The first four sources are examined here; experimental errors are treated under Methods.

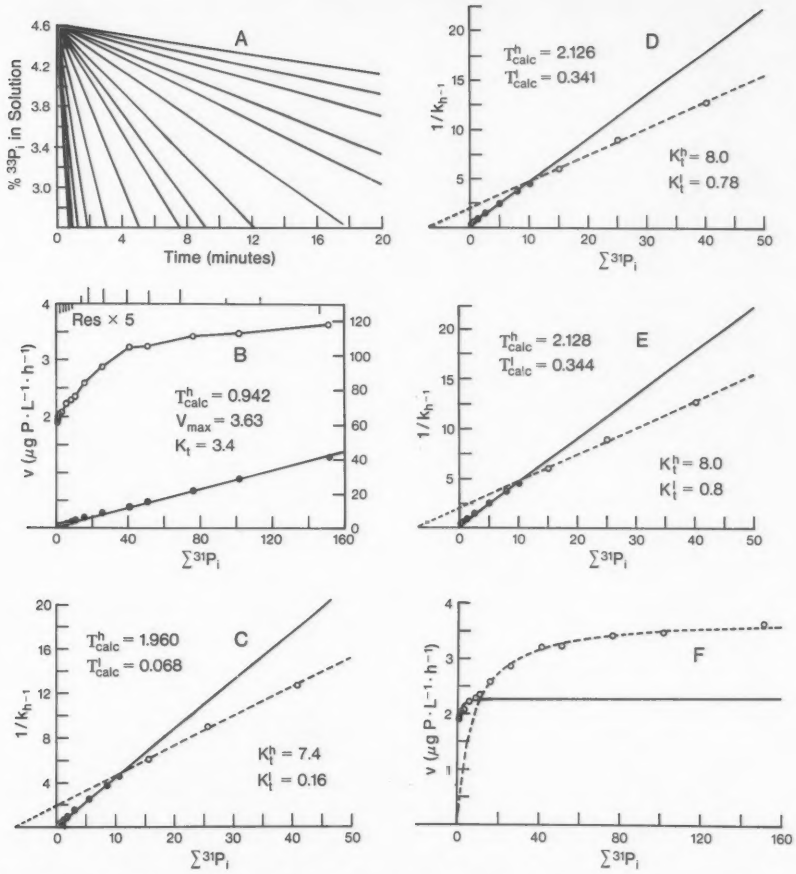


FIG. 3. Microbial $^{31}P_i$ uptake in a sample of offshore Lake Michigan water collected June 28, 1978, showing deviations from the simple Michaelis–Menten equation. (A) Regressions showing percentage loss of $^{33}P_i$ from solution versus time in subsamples. (B) v versus $\Sigma^{31}P_i$ concentration (open circles), linearization of uptake data using the Woolf transformation (solid circles), and residual values (Res) from the regression of $1/k$ on $\Sigma^{31}P_i$. Woolf plots showing nonlinearity and differences in T_{calc} and K_t obtained by back-extrapolating from "high" and "low" substrate regions using different $^{31}P_n$ estimates. (C) $^{31}P_n$ = MPPC (0.63 μg P·L^{-1}). (D) $^{31}P_n$ = MPPC × 10^{-2} (0.0063 μg P·L^{-1}). (E) $^{31}P_n$ = 0.0. (F) Comparison of measured v with predicted v constructed from uptake constants for "high" (broken line) and "low" substrate regions; $^{31}P_n$ = MPPC.

Experiments were designed to minimize errors arising from violation of steady-state conditions. Specifically, microbial biomass and $^{31}P_a$ must remain constant, and efflux of $^{31}P_i$-labeled compounds from cells must be negligible (McCarthy 1981). Although microbial growth rates are too low to result in increased biomass over 1- to 2-h incubations (0.1–0.3 doublings·d^{-1} for phytoplankton (S. J. Tarapchak, unpubl. data)), substantial amounts of $^{33}P_i$ can be taken up during the first 10–20 min in subsamples receiving $^{31}P_a < 1.0$ μg P·L^{-1}. To reduce this error and to avoid release and subsequent retention of labeled metabolites on filters (Lean 1973), we measured $^{33}P_i$ uptake by taking aliquots over short incubation times.

The optimum range and arrangement of substrate additions cannot be precisely defined for mixed populations with unknown kinetic constants (Endrenyi 1981). We followed a modified version of Cleland's (1967) scheme, where substrate additions are arranged geometrically over a range of 0.2 to 5.0·K_t, and assumed that species K_t could vary from 0.5 to 50 μg P·L^{-1} (Stross and Pemrick 1974; Nalewajko and Lean 1980). Additional subsamples below $^{31}P_a$ = 30 μg P·L^{-1} were usually included to define the nonlinear region more precisely.

Although kinetic constants are usually obtained by fitting transformed data by least-squares unweighted linear regression analysis (e.g. Halmann and Stiller 1974; Lean and White 1983), intercepts and particularly their estimated errors will be biased unless the error in $1/k$ is homoscedastic (Dowd and Riggs 1965; Li 1982). We tested replicate (N = 3) subsamples for this (see Methods). Analysis of 25 experiments showed that the error in estimating k increased with increasing k (Fig. 2). To elminate this bias, we used the relationship between k and its standard error to compute weights for the weighted linear regression of $1/k$ on $\Sigma^{31}P_i$ (Draper and Smith 1966).

Precise differences between T^h_{calc} and T^l_{calc} hinge on accurate

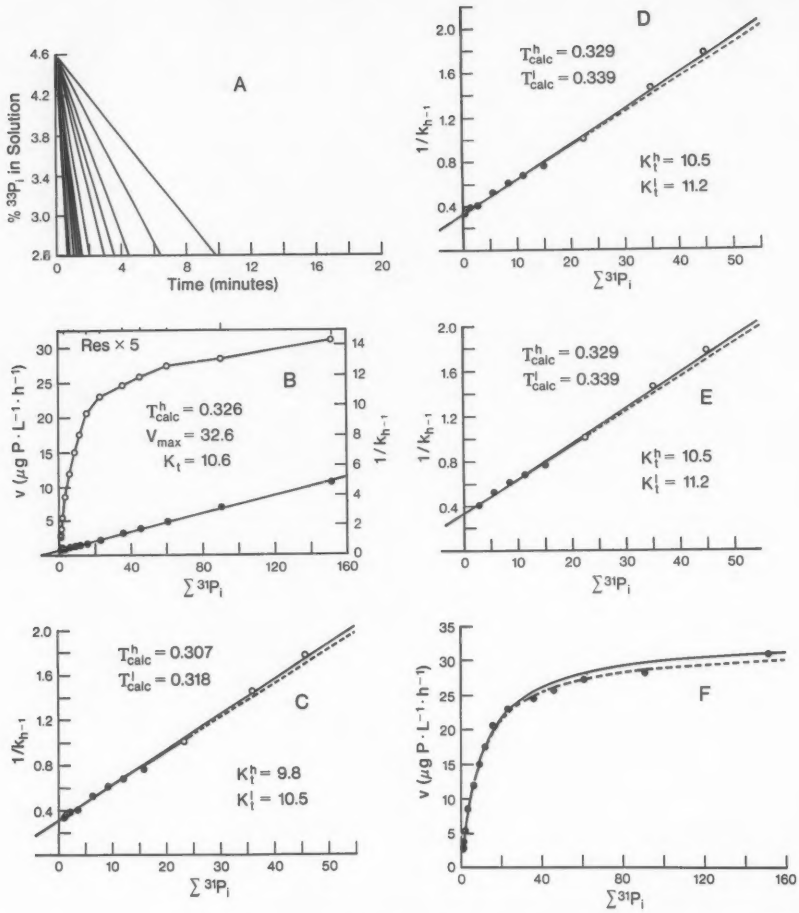


FIG. 4. Microbial $^{31}P_i$ uptake in a sample of offshore Lake Michigan water collected July 17, 1979, showing a fit to the simple Michaelis–Menten equation. Analysis is based on an arbitrary cutoff point of 20 μg P·L^{-1}; MPPC = 0.71 μg P·L^{-1}. See Fig. 3 legend for explanation of plots.

$^{31}P_n$ estimates (Williams 1973). Although there are no accurate methods for low-level $^{31}P_n$ estimation (Rigler 1968; Lean 1973; Paerl and Downes 1978; Stainton 1980; Tarapchak et al. 1982a), Williams' prediction can be tested if $^{31}P_n$ can be bounded. Maximum possible orthophosphate concentrations (MPPC) can be estimated from Rigler's (1966) method (Peters 1978; Smith and Kalff 1982), and the lowest possible value can be set at $^{31}P_n = 0$. For each experiment, $^{31}P_i$ uptake was analyzed at these concentrations and at MPPC × 10^{-1}, MPPC × 10^{-2}, and MPPC × 10^{-3}. Evidence that Williams' prediction holds is arbitrarily defined as a positive, statistically significant difference between T^h_{calc} and T^l_{calc} that cannot be eliminated by using $^{31}P_n$ estimates at two or more possible $^{31}P_n$ levels.

Methods

Sixty-two experiments were performed on water from Lake Michigan, a P-limited oligotrophic–mesotrophic lake (Schelske 1975). Samples were taken from May through October, 1976–80, at an offshore station 15 km west of Grand Haven, MI. Water was collected at evenly spaced depths in the epilimnion in 5-L Niskin bottles and mixed (1976) or at a depth of 4–6 m in a 20-L PVC Niskin bottle (1977–80). Within 20 min of collection, 200-mL subsamples were poured into twelve to sixteen 250-mL polycarbonate flasks that had been rinsed with sample to remove residual contamination and to saturate $^{31}P_i$ uptake sites. Flasks were placed in an incubator at ~70% incident solar radiation and maintained at in situ temperature for several minutes before starting experiments.

Subsamples were spiked with individual stock solutions of KH_2PO_4 and carrier-free orthophosphoric acid ($^{33}P_i$ in 0.02 mol HCl·L^{-1}, New England Nuclear (NEN), Boston, MA) prepared in double-distilled, deionized water. Solutions were prepared in serum bottles; 1.0-mL addition (made with an MLA micropipette) to subsamples gave final $^{31}P_a$ ranging from 0.08 or 0.175 μg P·L^{-1} to 151 or 250 μg P·L^{-1}. Tests based on $^{33}P_i$ loss from solution showed that $^{31}P_a$ was accurate. Less than 1.0% of the $^{31}P_i$ sorbed to the serum bottles. Each subsample was mixed with a magnetic stirring bar to ensure rapid dispersion of the spike. To reduce errors caused by reduction in $^{31}P_i$ pool size, experiments were conducted in two sets. Subsamples spiked with <3.0 μg $^{31}P_a$ (where $^{33}P_i$ uptake was rapid)

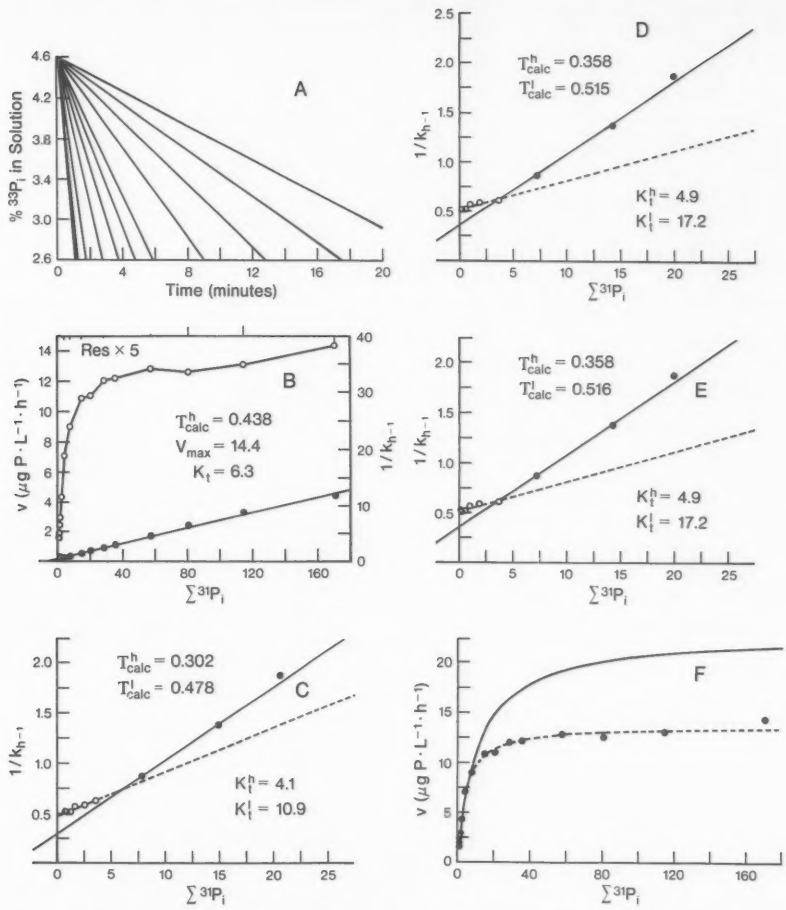


FIG. 5. Microbial $^{31}P_i$ uptake in a sample of offshore Lake Michigan water collected August 20, 1980, showing a deviation from the simple Michaelis–Menten equation opposite to that predicted by Williams (1973); MPPC = 0.66 μg P·L^{-1}. See Fig. 3 legend for explanation of plots.

were usually incubated for 1–3 h; other flasks were incubated for 2–4 h. Generally, six to nine aliquots were removed over the first 5–10 min from the first set and over the first 20–30 min from the second set.

Subsamples were filtered and assayed, and k was computed as follows. Within 2–3 s after adding the spike, 10-mL aliquots were withdrawn and filtered onto 0.45-μm Millipore filters (25 mm in diameter) at 150 ± 30 mmHg using a six-place Millipore filtration manifold (8–10 s elapsed time after the spike). Filters were counted in Aquasol (NEN) in a Beckman model LS 150 liquid scintillation spectrometer (counting efficiency 81–86%). Total $^{33}P_i$ estimates were obtained by assaying three or more 1.0-mL aliquots from each subsample. Counts were corrected for isotopic decay when elapsed time between assay of the first and last vial gave more than a 1.0% difference. The value of k was computed as the initial slope of the line on a plot of ln % $^{31}P_i$ in solution versus time in minutes using least-squares linear regression and converted to an hourly rate by multiplying by 60.

Experimental errors that can bias k at low $^{31}P_a$ were checked. (1) The value of k can be overestimated by >100% at low $^{31}P_a$ because $^{33}P_i$ is sorbed by Millipore filters (Lean 1976; S. J. Tarapchak, unpubl. data). This artifact was eliminated by simultaneously filtering aliquots through two filters and subtracting the activity of the bottom filter (sorption) from that of the top filter (sorption plus biologic uptake). (2) Filtration can result in release of intracellular $^{33}P_i$ as cells are damaged by impingement (Lean 1976; Tarapchak et al. 1982b). Vacuum pressure tests on lake water samples (N = 13) and on laboratory monocultures of fragile algae (*Cryptomonas* and *Ochromonas*) showed that $^{31}P_i$ retention on filters was essentially constant (<7% of the mean) between 75 and 250 mmHg. (3) Chemiluminance and/or exposure to bright light can severely elevate activity for 6–8 h following Aquasol addition. Vials were manually shaken and sonicated several times over 24 h to insure uniform dispersion of tracer, stored in darkness for 24–48 h, and then loaded into the counter in near darkness and counted several hours later. (4) Abiotic $^{33}P_i$ uptake can grossly overestimate k (Rigler 1973), but tests showed that <0.2% is taken up by this process (Tarapchak et al. 1981). Conversely, differences between T^h_{calc} and T^l_{calc} at low $^{31}P_a$ can be masked if the mass of the $^{31}P_i$ spike increases $\Sigma^{31}P_i$ pool size

TABLE 1. Comparison of percentage differences between T^h_{calc} and T^l_{calc} for selected simulation runs based on 30 species, a $V_{max}:K_t$ of 5, and different ranges of species K_t and relative abundance values. Results in the first of each pair of rows are based on a uniform spacing of K_t values, where K_t values increase uniformly over the entire specified K_t and abundance range. The second of each pair of rows of values is based on uniformly spaced K_t values within each order of magnitude over the specified K_t range. Abundance values in all runs are spaced uniformly over the specified range. Abundance values in columns 2 through 4 decrease with increasing K_t; values in the last three columns increase with increasing K_t.

Species K_t range	Relative abundance						
	Equal	$10 \rightarrow 1$	$100 \rightarrow 1$	$1000 \rightarrow 1$	$1 \rightarrow 10$	$1 \rightarrow 100$	$1 \rightarrow 1000$
10 ($0.1 \rightarrow 1$)	24	32	31	31	12	10	9
	—	—	—	—	—	—	—
100 ($0.1 \rightarrow 10$)	34	51	52	52	16	13	12
	109	—	197	196	—	49	48
1000 ($0.1 \rightarrow 100$)	36	54	55	55	16	13	13
	213	—	514	512	—	97	96

(Rigler 1973). Although $^{33}P_i$ mass can be calculated from dpm, $^{31}P_n$ is unknown. Therefore, we empirically tested for isotopic dilution by charting the time course of carrier-free $^{33}P_i$ uptake in flasks spiked with a 1000-fold difference in activity. The slopes and intercepts of curves in 12 experiments (two each month) were statistically nonsignificant (*t*-test, $P > 0.4$, Brownlee 1965).

Maximum possible PO_4-P concentrations (MPPC) were estimated by Rigler's (1966) method (Tarapchak and Rubitschun 1981). Successively lower assumed $^{31}P_n$ were used until the curve on a plot of ν versus $\Sigma^{31}P_i$ swung toward the origin (Peters 1978). Precision of MPPC estimation in 12 replicated experiments ($N = 3$) was high (SE < 8.5%). Glassware was washed in hot water and Liquinox (Alconox, Inc., New York), a phosphate-free detergent, rinsed with tap water, soaked in concentrated HNO_3 for at least 12 h, and rinsed six times in distilled, deionized water.

Results and Discussion

Types of Kinetic Systems

Uptake of $^{31}P_i$ usually failed to fit the simple Michaelis–Menten equation. Three distinct types of systems were detected. Sixty-five percent of the experiments showed nonlinearity as predicted by Williams (1973), 20% gave acceptable fits to equation (1), and 15% revealed an unexpected deviation from equation (1). The first type is characterized by steeply sloped ν versus $\Sigma^{31}P_i$ curves with nonlinearity beginning between 5 and 20 $\mu g\ ^{31}P_i \cdot L^{-1}$, where differences between T_{calc} and between K_t normally range from 100 to 2000%. In an experiment where the maximum deviation was observed (Fig. 3), differences between T^h_{calc} and T^l_{calc} and between K^h_t and K^l_t (using MPPC as the $^{31}P_n$ estimate) are 2765% (*t*-test, $P < 0.0001$) and 4603%, respectively (Fig. 3C), but decrease to between 500 and 600% (*t*-test, $P < 0.0001$) and 900 and 1000%, respectively, when lower $^{31}P_n$ are used (Fig. 3D, 3E).

The degree to which ν is underestimated at ambient $^{31}P_n$ can be illustrated by substituting each of the two sets of V_{max} and K_t values into equation (1) and constructing predicted uptake curves. For the experiment in Fig. 3, predicted ν using constants from the "low" substrate region gives a better fit to measured ν at low $\Sigma^{31}P_i$ than predicted ν based on constants from the "high" substrate region (Fig. 3F), and vice versa. Assuming that $^{31}P_n$ equals MPPC, ν is underestimated by 520%. For 40 experiments yielding nonlinear Woolf plots, ν on average was underestimated by ~300% with values ranging to 840%.

These kinetic systems are not artifacts caused by imprecise $^{31}P_n$ estimation or poor reproducibility. Although the exact error cannot be calculated because true $^{31}P_n$ is unknown, our results show that deviations from model uptake occur frequently. On average, T^h_{calc} exceeded T^l_{calc} by 650% (based on $^{31}P_n$ = MPPC) or by 425% (based on $^{31}P_n = 0$). Experiments showing deviations <1000% were relatively insensitive (<50%) to variations in $^{31}P_n$. However, when deviations were >1500%, percentage differences were usually smaller when $^{31}P_n$ values below MPPC were used (Fig. 3). Replication ($N = 3$) of six experiments yielded relatively high precision (range of percentage SE of the mean): T^l_{calc} (3–8%), K^l_t (3–10%), T^h_{calc} (6–13%), K^h_t (6–15%), indicating that differences between T_{calc} must be below ~25% before deviations from equation (1) can be attributed to measurement error.

Uptake of $^{31}P_i$ was regarded as conforming to the simple Michaelis–Menten equation when differences between T_{calc} were statistically nonsignificant (*t*-test, $P > 0.10$) at $^{31}P_n$ ranging between 2 and 50 $\mu g\ P \cdot L^{-1}$ at two or more assumed $^{31}P_n$ levels. This type of system, illustrated in Fig. 4, shows that back-extrapolating from "high" and "low" substrate regions gives curves virtually superimposed on one another (Fig. 4C–4E), with statistically nonsignificant (*t*-test, $P > 0.770$) differences between T_{calc}. As expected, predicted ν using constants from "high" and "low" substrate regions also fits measured ν very well (Fig. 4F). These uptake systems usually yielded statistically nonsignificant differences ($P > 0.1$) between T_{calc} at all possible $^{31}P_n$.

The third type of system is the opposite of that predicted by Williams. Extrapolation from the "high," rather than the "low," substrate region yields numerically lower uptake constants. This system, illustrated in Fig. 5, shows a distinct separation of curves in Woolf plots. The T_{calc} estimates are statistically significant (*t*-test, $P < 0.0003$). Nonlinearity usually begins at relatively high $\Sigma^{31}P_i$ ($\geq 25\ \mu g\ P \cdot L^{-1}$); differences between T_{calc} range from 50 to 150%, and predicted ν based on constants from "high-level" extrapolation fit measured ν relatively well (Fig. 5F). Uptake constants are relatively insensi-

TABLE 2. Comparison of percentage differences between T^h_{calc} and T^l_{calc} for selected simulation runs based on "skewed" distributions. Analyses are based on 30 species, a $V_{max}:K_t$ of 5, a 1000-fold range in species K_t values, and variable or equal species abundances. Cont = distributions where, for each order of magnitude, K_t values are uniformly spaced and abundance values increase or decrease; Clmp = clumped distributions with seven species in each group; Equal = equal abundance.

Run	K_t range	Relative abundance	% deviation in T_{calc}
1A	Cont (0.05 → 50)	Cont (1000 → 1)	1771
1B	Cont (0.05 → 50)	Cont (1 → 1000)	22
2A	Cont (0.05 → 50)	Clmp (100, 10, 1)	1642
2B	Cont (0.05 → 50)	Clmp (1, 10, 100)	39
3A[a]	Clmp (0.05, 50)	Equal (1)	100
3B	Clmp (0.05, 0.5, 5, 50)	Equal (1)	227
3C	Clmp (0.05, 0.5, 5, 50)	Clmp (1000, 100, 10, 1)	7607
3D	Clmp (0.05, 0.5, 5, 50)	Clmp (1, 10, 100, 1000)	9
3E	Clmp (0.05, 0.5, 5, 50)	Cont (1000 → 1)	7572
3F	Clmp (0.05, 0.5, 5, 50)	Cont (1000 → 1)[b]	669

[a]Based on 28 species.
[b]Uniformly decreasing abundance values spaced over the entire specified K_t range.

tive to assumed $^{31}P_n$. Precision estimates gave results comparable with those cited above.

Contrasts with Williams' Predictions

Our results support Williams' prediction. However, differences between T_{calc} in nearly one half of the experiments exceeded the predicted maximum of 213%, casting suspicion on our measurements or on Williams' assumptions. Because experimental errors can be ruled out (see Experimental Design), the maximum predicted deviation could be underestimated if (1) equation (1) fails to characterize $^{31}P_i$ uptake by individual species, (2) the assumed range of species K_t values is narrower than in natural assemblages, or (3) variable species' abundance affects deviations from model uptake. The first explanation should not account for the discrepancy, provided that species have single transport systems, because equation (1) is a generally accepted model for microbial $^{31}P_i$ uptake (Button 1978; Rosen 1978). The second is unlikely, since Williams used up to a 1000-fold range in the number of species, K_t, and V_{max} and allowed the distribution of K_t and V_{max} to vary in different ways. Hence, variable species abundance might be responsible.

Simulation Analysis

We modeled equation (1) to test the effects of variable species K_t and abundance on deviations in $^{31}P_i$ uptake from the simple Michaelis–Menten equation. Uptake velocity for a microbial assemblage was calculated by computing v for each species (normalized for abundance) and summing the values. The T_{calc} values were computed by evaluating the limiting expressions for $1/k$ and the slope of $1/k$ (as functions of $\Sigma^{31}P_i$) as $\Sigma^{31}P_i$ approaches 0 (T^l_{calc}) and ∞ (T^h_{calc}). This yielded parameters specifying tangent lines to the curve at $\Sigma^{31}P_i = 0$ and at $\Sigma^{31}P_i = \infty$. The y-axis intercepts of these lines at $\Sigma^{31}P_i = 0$ give T^l_{calc} and T^h_{calc}, respectively. Simulations were carried out in two sets. First, the effects of variable species K_t and relative abundance distributions on deviations from a linear extrapolation of uptake curves from the "high" substrate region were explored. Second, possible causes for the experimentally observed discrepancies were examined.

For the first set, K_t values were spaced uniformly over one, two, or three orders of magnitude (beginning with a K_t of 0.1 μg P·L^{-1}), and species abundances were set equal (to test Williams' prediction) or allowed to range 10-, 100-, and 1000-fold in either increasing or decreasing order with respect to the K_t arrangement. The $V_{max}:K_t$ for each species was set at 5.0, and 30 species were used in all runs (see below). Results confirm Williams' (1973) prediction and also demonstrate that deviations from model uptake are affected by species abundance (Table 1). For runs based on equal abundance, differences in T_{calc} never exceeded 36% when K_t values were uniformly spaced. However, deviations from model uptake increased dramatically when equal numbers of species K_t values were spaced uniformly *within* each order of magnitude. The maximum deviation predicted by Williams, based on a 1000-fold range in K_t where values were uniformly spaced within each of three orders of magnitude, was verified (Table 1; Fig. 6A).

Variations in species abundance substantially affect T_{calc} estimates (Table 1). When the lowest K_t value (0.1 μg P·L^{-1}) was assigned the highest abundance, differences in T_{calc} were much greater than those obtained when abundances were set equal (especially for runs where K_t values were spaced uniformly within orders of magnitude). For example, the error in T_{calc} was 55% based on a 1000-fold K_t and abundance range when K_t values were uniformly distributed, but increased to 500% when K_t values were uniformly spaced within each order of magnitude (Fig. 6B). Conversely, when abundances were arranged so that species with the lowest K_t were *least* abundant, deviations from model uptake were below those obtained when abundances were set equal. Hence, relative species abundance must also be considered in examining causes of discrepancies from equation (1).

Simulating $^{31}P_i$ uptake by natural assemblages is complicated because the range of K_t values and their distribution with respect to abundance is unknown (Smith and Kalff 1982, 1983). Our analyses are based on 30 species, a $V_{max}:K_t$ value of 5, a K_t range of 0.05–50 μg P·L^{-1}, and two types of theoretical distributions. This number of species is reasonable because autoradiographic analysis revealed that at least 30 species in Lake Michigan take up $^{31}P_i$ (S. J. Tarapchak, unpubl. data).

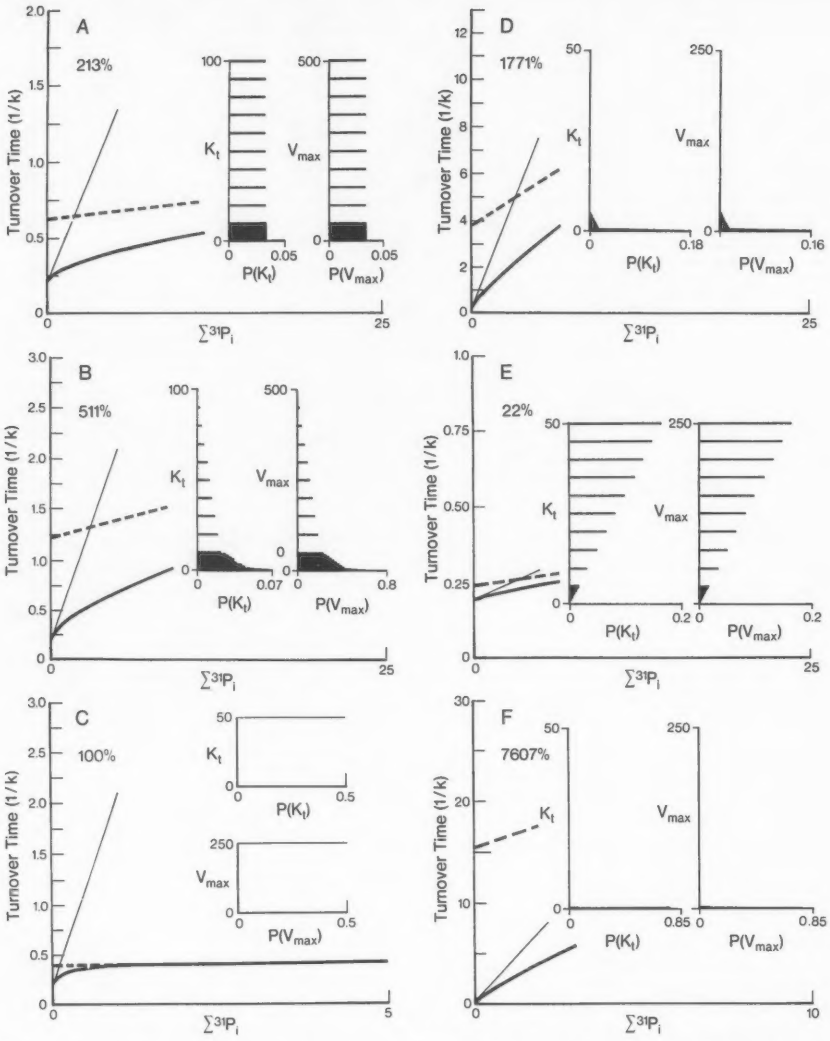


FIG. 6. Results of selected simulation runs based on a 1000-fold range in species K_t and/or abundance showing percentage deviations between T_{calc} obtained by back-extrapolating curves from "high" and "low" substrate regions in Woolf plots. (A) K_t values spaced uniformly within each order of magnitude and equal abundance. (B) K_t values spaced uniformly within each order of magnitude and abundances distributed uniformly over a 1000-fold range. (C) Equal K_t values in each of two groups with equal abundance. (D) "Left-skewed" K_t and abundance distribution. (E) "Right-skewed" K_t and abundance distribution. (F) "Clumped-left" K_t and abundance distribution. $P(K_t)$ and $P(V_{max})$ refer to associated fraction of total abundance.

The $V_{max}:K_t$ approximates the average ratio calculated from our experiments. A 1000-fold range in K_t was chosen on the assumption that species K_t would vary by a factor of two smaller than the lowest (0.1 μg $P \cdot L^{-1}$) to twice the highest (~20 μg $P \cdot L^{-1}$) assemblage K_t estimate.

Two types of distributions were constructed. First, we assumed that species could compete for $^{31}P_i$ as a single limiting resource across a concentration gradient, where only small changes in concentration favor one species over another (Tilman 1982). Species K_t and abundances were uniformly spaced within each of three orders of magnitude. For "left-skewed" distributions, the species with the lowest K_t was assigned highest abundance, while for the "right-skewed" distributions, the species with the lowest K_t was assigned lowest abundance. Second, assemblages may be composed of groups of microorganisms, each with similar K_t and abundance values, where relatively large differences in $^{31}P_i$ are necessary for species in one group to outcompete a species in another (Tilman 1981). "Clumped" distributions were constructed by assigning different species K_t and abundance values to each of two, three, or four groups. For "clumped-left" arrangements, the species group with the lowest K_t was assigned highest

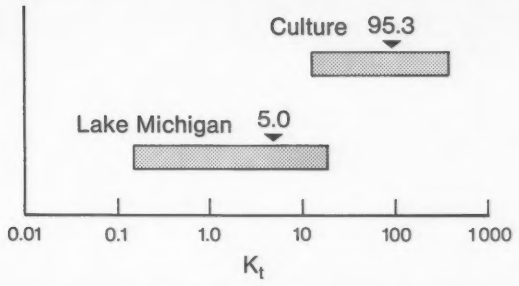


FIG. 7. Comparison showing high and low range estimates and mean K_t values of $^{31}P_i$ uptake by Lake Michigan microbial assemblages (N = 62) and by microorganisms in laboratory culture (N = 38).

abundance, while "clumped-right" arrangements are groupings where the lowest K_t values were assigned the lowest abundance.

Results reveal that "left-skewed" and "clumped-left" distributions produced deviations that approached (~1800%) or exceeded (~7500%) the maximum experimentally detected deviation in Lake Michigan (Table 2; Fig. 6D, 6F). The error in estimating T_{calc}, however, was drastically reduced when abundances were redistributed such that the species with the highest K_t was assigned the highest abundance. For example, the "right-skewed" and the "clumped-right" distributions yielded values of only 22% (Fig. 6E) and 9% (run 3D, Table 2), respectively.

Caution must be exercised in using simulations to identify K_t and abundance arrangements that cause large discrepancies from model uptake. For example, our analyses implicitly assume that species have single rather than multiple transport systems, that complex metabolic regulation (e.g. feedback inhibition) of $^{31}P_i$ uptake does not occur, and that species transport systems are of equal capacity (Button 1978). If these conditions are not seriously violated, large deviations from model uptake can be simulated by "skewed" or "clumped" distributions where species with low K_t values are most abundant. However, precise knowledge of the structure of communities must await accumulation of data on uptake constants of natural populations (e.g. Smith and Kalff 1982).

Microbial Uptake Systems in Lake Michigan

Our analyses provide a theoretical framework for examining potential causes of two observed uptake systems. Systems showing positive deviations (Fig. 3) occur during spring, early summer, and late fall when assemblage K_t values are low (0.1−3.0 μg $P \cdot L^{-1}$) and diatoms are dominant (>70%). According to Williams, large deviations from model uptake occur when assemblages are composed of species with K_t values differing by ≥100% when $^{31}P_n$ is less than assemblage K_t. Our analyses extend these predictions. First, variable species abundance causes much larger deviations than predicted. Second, the error in T_{calc} can be relatively large when $^{31}P_n$ is greater than assemblage K_t. For example, the "left-skewed" distribution that produced an error of 1771% (Fig. 6D) at $\Sigma^{31}P_n = 0$ yielded errors of about 750, 500, and 400% at $^{31}P_n$ corresponding to one-half assemblage K_t, the assemblage K_t (0.54 μg $P \cdot L^{-1}$), and twice the assemblage K_t, respectively. Although we cannot deduce the precise range of species K_t in Lake Michigan, deviations >1000% could result from "skewed" or "clumped" distributions, where species with low K_t values are abundant. Our simulations also show that for "skewed" abundance distributions, species K_t must vary 100- to 1000-fold to achieve the maximum deviation detected in Lake Michigan.

Uptake systems that fit equation (1) (Fig. 4) occur during mid- to late summer when assemblage K_t values are relatively high (5 and ~20 μg $P \cdot L^{-1}$) and green and blue-green algae are dominant (>70%). According to Williams (1973), ν will fit equation (1) if $^{31}P_n$ is greater than assemblage K_t, or when $^{31}P_n$ is less than assemblage K_t if all species have identical K_t. We rule out the first possibility because K_t values in summer are 5−10 times higher than MPPC (Tarapchak and Rubitschun 1981). Although we cannot dismiss the second possibility, it is probable that potentially large deviations from model uptake resulting from a wide range in species K_t are offset by dominance of species with high K_t's (Table 2).

The uptake system opposite to the one predicted by Williams (Fig. 5) also occurs during summer. The discrepancy from model uptake results from rapid $^{31}P_i$ uptake at relatively high $\Sigma^{31}P_a$. Although we are uncertain of the cause, one explanation is that some species have relatively high thresholds and, therefore, do not take up $^{31}P_i$ until relatively high levels are added (cf. Brown and Button 1979).

Comparisons with Culture Studies

Comparisons between K_t values for Lake Michigan assemblages with those measured in laboratory monocultures show that the range for natural assemblages is shifted nearly two orders of magnitude lower (Fig. 7). The K_t values of algae, bacteria, and fungi vary between 11 and 364 μg $P \cdot L^{-1}$ (mean = 95) (based on 38 measurements from a literature search through 1982), whereas those for natural assemblages range from 0.15 to 19.4 μg $P \cdot L^{-1}$ (mean = 5.0, N = 62). Therefore, some natural populations must have K_t values substantially <0.1 μg $P \cdot L^{-1}$, because assemblage estimates represent a weighted average of all species. These results suggest that $^{31}P_i$ transport systems of natural and cultured microbes are dissimilar.

There are two possible explanations for the high K_t of cultured populations. First, microorganisms may have multiple transport systems (Brown et al. 1978), but the range in $^{31}P_a$ may be too high to detect a high-affinity system. Second, high-affinity transport systems of natural populations are lost, either through genetic selection or by physiologic adaptation, when microorganisms are grown under relatively high nutrient regimes (Dugdale et al. 1981). Although the first possibility cannot be discounted, examination of studies demonstrating multiple transport provides no evidence for the existence of another system operating at lower substrate levels.

Microbial populations in P-limited waters, therefore, apparently develop extremely high-affinity $^{31}P_i$ transport systems. This is consistent with physiologic properties of microorganisms — microbes characteristically adapt to P stress by synthesizing alternate high-affinity transport systems at the expense of reductions in macromolecular synthesis (Tempest and Neijssel 1976; Harder and Dijkhuizen 1983). Our results differ from culture studies only in that the K_t's are at least an order of magnitude below those measured in culture. Measurements on the kinetics of $^{31}P_i$ uptake by natural populations suggest that the phenomenon is generalized. For example, Smith and Kalff (1982) reported K_t from 0.31 to 3.4 μg $P \cdot L^{-1}$ as measured by autoradiography for several algae in lake water chemostats, and

Stross and Pemrick (1974) detected K_t's of 0.31 and 1.6 μg $P \cdot L^{-1}$ for the diatoms *Tabellaria* and *Fragilaria*, respectively. These estimates, coupled with observed K_t's for Lake Michigan assemblages, strongly suggest that microorganisms synthesize transport systems that allow efficient exploitation of chronically low bulk $^{31}P_n$.

In summary, our studies show that $^{31}P_i$ uptake by natural microbial assemblages in Lake Michigan usually deviates from the simple Michaelis–Menten equation. This could be caused by the presence of species populations with widely different K_t and abundance values.

Acknowledgments

We thank B. J. Eadie, W. S. Gardner, P. F. Landrum, D. Scavia, and H. A. Vanderploeg for suggestions on the manuscript. Greg Houttemann helped program the simulation routine and Elizabeth Cichocki kindly assisted in data analysis.

References

BROWN, E. J., AND D. K. BUTTON. 1979. Phosphate-limited growth kinetics of *Selenastrum capricornutum* (Chlorophyceae). J. Phycol. 15: 305–311.

BROWN, E. J., R. F. HARRIS, AND J. F. KOONCE. 1978. Kinetics of phosphate uptake by aquatic microorganisms: deviations from a simple Michaelis–Menten equation. Limnol. Oceanogr. 23: 27–34.

BROWNLEE, K. A. 1965. Statistical theory and methodology in science and engineering. John Wiley & Sons, Inc., New York, NY. 590 p.

BUTTON, D. K. 1978. On the theory of control of microbial growth kinetics by limiting nutrient concentrations. Deep-Sea Res. 25: 1163–1177.

CLELAND, W. 1967. The statistical analysis of enzyme kinetic data. Adv. Enzymol. 29: 1–32.

DOWD, J. E., AND D. S. RIGGS. 1965. A comparison of estimates of Michaelis–Menten kinetic constants from various linear transformations. J. Biol. Chem. 240: 863–869.

DRAPER, N., AND H. SMITH. 1966. Applied regression analysis. John Wiley & Sons, Inc., New York, NY. 407 p.

DUGDALE, R. C., B. H. JONES JR., J. J. MACISAAC, AND J. J. GOERING. 1981. Adaptation of nutrient assimilation, p. 234–250. *In* T. Platt [ed.] Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210: 346 p.

ENDRENYI, L. [ED.] 1981. Kinetic data analysis: design and analysis of enzyme and pharmacokinetic experiments. Plenum Press, New York, NY.

HALMANN, M., M. STILLER. 1974. Turnover and uptake of dissolved phosphate in fresh water: a study of Lake Kinneret. Limnol. Oceanogr. 19: 774–783.

HARDER, W., AND L. DIJKHUIZEN. 1983. Physiologic responses to nutrient limitation. Annu. Rev. Microbiol. 37: 1–23.

LEAN, D. R. S. 1973. Phosphorus dynamics in lake water. Science (Wash., DC) 1979: 678–680.

1976. Phosphorus kinetics in lake water: influence of membrane filter pore size and low-pressure filtration. J. Fish. Res. Board Can. 33: 2800–2804.

LEAN, D. R. S., AND F. R. PICK. 1981. Photosynthetic response of lake plankton to nutrient enrichment: a test for nutrient limitation. Limnol. Oceanogr. 26: 1001–1019.

LEAN, D. R. S., AND E. WHITE. 1983. Chemical and radiotracer measurements of phosphorus uptake by lake plankton. Can. J. Fish. Aquat. Sci. 40: 147–155.

LEHMAN, J. T., AND C. D. SANDGREN. 1982. Phosphorus dynamics of the procaryotic nannoplankton in a Michigan lake. Limnol. Oceanogr. 27: 828–838.

LEVINE, S. N., AND D. W. SCHINDLER. 1980. Radiochemical analysis of orthophosphate concentration and seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 335–341.

LI, W. K. W. 1982. Consideration in errors in estimating kinetic parameters based on Michaelis–Menten formalism in microbial ecology. Limnol. Oceanogr. 28: 185–190.

MCCARTHY, J. J. 1981. The kinetics of nutrient utilization, p. 211–233. *In* T. Platt [ed.] Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210: 346 p.

NALEWAJKO, C., AND D. R. S. LEAN. 1980. Phosphorus, p. 235–258. *In* E. Morris [ed.] The physiological ecology of phytoplankton. University of California Press, Berkeley, CA.

NALEWAJKO, G., K. LEE, AND H. SHEAR. 1981. Phosphorus kinetics in Lake Superior: light intensity and phosphate uptake in algae. Can. J. Fish. Aquat. Sci. 38: 224–232.

PAERL, H. W., AND M. T. DOWNES. 1978. Biological availability of low versus high molecular weight reactive phosphorus. J. Fish. Res. Board Can. 35: 1639–1643.

PETERS, R. H. 1978. Concentration and kinetics of phosphorus fractions in water from streams entering Lake Memphremagog. J. Fish. Res. Board Can. 35: 315–328.

RIGLER, F. H. 1966. Radiobiological analysis of inorganic phosphorus in lake water. Verh. Int. Ver. Limnol. 16: 465–470.

1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures inorganic phosphorus in lake water. Limnol. Oceanogr. 13: 7–13.

1973. A dynamic view of the phosphorus cycle in lakes, p. 539–572. *In* E. J. Griffith, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] Environmental phosphorus handbook. John Wiley & Sons, Inc., New York, NY.

ROSEN, B. P. 1978. Bacterial transport. Marcel Dekker, New York, NY. 684 p.

SCHELSKE, C. L. 1975. Silica and nitrate depletion as related to rate of eutrophication in Lake Michigan, Lake Huron, and Lake Superior, p. 277–298. *In* A. D. Hasler [ed.] Coupling of land and water systems. Springer, New York, NY.

SMITH, R. E., AND J. KALFF. 1982. Size-dependent phosphorus uptake kinetics and cell quota in phytoplankton. J. Phycol. 18: 275–284.

1983. Competition for phosphorus among cooccurring freshwater phytoplankton. Limnol. Oceanogr. 28: 448–464.

STAINTON, M. P. 1980. Errors in molybdenum blue methods for determining orthophosphate in fresh water. Can. J. Fish. Aquat. Sci. 37: 472–478.

STROSS, R. G., AND S. M. PEMRICK. 1974. Nutrient uptake kinetics in phytoplankton: a basis for niche separation. J. Phycol. 10: 164–169.

TARAPCHAK, S. J., S. M. BIGELOW, AND C. RUBITSCHUN. 1982a. Overestimation of orthophosphorus concentrations in surface waters of southern Lake Michigan: effects of acid and ammonium molybdate. Can. J. Fish. Aquat. Sci. 39: 296–304.

1982b. Soluble reactive phosphorus measurements in Lake Michigan: filtration artifacts. J. Great Lakes Res. 8: 550–557.

TARAPCHAK, S. J., AND C. RUBITSCHUN. 1981. Comparison of soluble reactive phosphorus and orthophosphorus concentrations at an offshore station in southern Lake Michigan. J. Great Lakes Res. 7: 290–298.

TARAPCHAK, S. J., D. R. SLAVENS, AND L. M. MALONEY. 1981. Abiotic versus biotic uptake of radiophosphorus in lake water. Can. J. Fish. Aquat. Sci. 38: 889–895.

TEMPEST, D. W., AND O. M. NEIJSSEL. 1976. Microbiological adaptation to low-nutrient environments, p. 283–296. *In* A. C. R. Dean et al. [ed.] Continuous culture 6: applications and new fields. Ellis Harwood Ltd., Chichester.

TILMAN, D. 1981. Experimental tests on resource competition theory using four species of lake Michigan algae. Ecology 62: 802–815.

1982. Resource competition and community structure. Monographs in population biology. Vol. 17. Princeton University Press, Princeton, NJ.

WILLIAMS, P. J. L. 1973. The validity of the application of simple kinetic analysis to heterogeneous microbial populations. Limnol. Oceanogr. 18: 159–164.

WRIGHT, R. T., AND J. E. HOBBIE. 1966. Use of glucose and acetate by bacteria and algae in aquatic ecosystems. Ecology 47: 447–464.

Light History, Phosphorus Status, and the Occurrence of Light Stimulation or Inhibition of Phosphate Uptake in Lake Superior Phytoplankton and Bacteria

C. Nalewajko and B. Paul[1]

Life Sciences Division, Scarborough Campus, University of Toronto, Scarborough, Ont. M1C 1A4

K. Lee

Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

and H. Shear

Department of Fisheries and Oceans, Fish Habitat Branch, Ottawa, Ont. K1A 0E6

Nalewajko, C., B. Paul, K. Lee, and H. Shear. 1986. Light history, phosphorus status, and the occurrence of light stimulation or inhibition of phosphate uptake in Lake Superior phytoplankton and bacteria. Can. J. Fish. Aquat. Sci. 43: 329–335.

Phosphate uptake in Lake Superior was stimulated by light on 17 out of 34 occasions, inhibited on 10, and unaffected on 7. In a stepwise multiple regression model the variables explaining most of the variance in the light effect on phosphate uptake were, in decreasing order of importance, the light history as estimated by hours of sunshine in previous 3 d, phosphate turnover time, phytoplankton biovolume, and time of day. Stimulation was most common in spring at inshore stations, while inhibition occurred mainly in spring at offshore stations. We suggest that light-limited but phosphorus-sufficient phytoplankton show the former, but extremely low light adapted populations, the latter response. We discovered an apparent diurnal pattern in the response, with maximal stimulation by light during daylight hours and inhibition predominating at sunrise and sunset.

Nous avons noté, au cours d'un total de 34 observations, que la lumière avait eu pour effet de stimuler l'assimilation du phosphate à 17 reprises et de l'inhiber à 10 reprises, l'effet ayant été nul à 7 reprises. Les variables d'un modèle de régression multiple par étapes expliquant la plus grande partie de la variance étaient, par ordre décroissant d'importance, l'éclairement antérieur estimé à partir du nombre d'heures d'ensoleillement au cours des 3 jours précédents, le temps de renouvellement du phosphate, le biovolume du phytoplancton et l'heure. Au printemps, la stimulation était plus fréquente aux stations près des rives tandis que l'inhibition se produisait surtout aux stations du large. Nous formulons l'hypothèse que le phytoplancton limité par l'éclairement mais non par le phosphore présentait la première réponse, la seconde étant présentée par les populations très fortement limitées par l'éclairement. Nous avons noté une tendance apparente de la réponse : la stimulation par la lumière était maximale durant les heures de clarté et l'inhibition prédominait au lever et au coucher du soleil.

Received August 31, 1984
Accepted October 2, 1985
(J7942)

Reçu le 31 août 1984
Accepté le 2 octobre 1985

Evidence that light stimulates phosphate uptake in phytoplankton was deemed not to be unequivocal by Cembella et al. (1984) on the basis of pre-1983 literature, but has been strengthened somewhat by several more recent reports (Kuenzler et al. 1979; Lemasson et al. 1980; Nalewajko and Lee 1983; Rivkin and Swift 1982; Nalewajko and Garside 1983) and by reports not included in that article. Of particular interest is the demonstration (Nalewajko and Lee 1983) that significant stimulation occurs in apparently phosphorus-limited populations. Earlier, Kuenzler et al. (1979) noted that darkening decreased phosphate uptake in plankton low in phosphate to a greater extent than in phosphate-rich plankton. This challenges the conclusions reached by Healey (1973) and Lean and Pick (1981), among others, that high phosphorus concentration is the prime prerequisite for light to stimulate phosphate uptake.

In spite of the accumulating evidence for stimulation by light of phosphate uptake, it is not clear under what conditions phosphate uptake in phytoplankton is light sensitive. Most researchers have focused on the phosphorus status as the crucial variable, and the prevailing understanding, based mainly on algal cultures, is that high phosphorus, or at least nonlimiting phosphorus supply, is a necessary prerequisite for light stimulation to occur (Cembella et al. 1984).

Except for Kuenzler et al. (1979), Nalewajko et al. (1981), and Nalewajko and Lee (1983), the importance of light history to the magnitude of the subsequent stimulation of phosphate uptake by light has not been taken into account. Our interest in light history as an important variable arose from experiments with both algal cultures and natural phytoplankton populations. We demonstrated that light stimulated phosphate uptake in cultures of *Chlorella* grown in low light to a greater extent than in cultures grown in high light (Nalewajko et al. 1981).

[1]Present address: Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1.

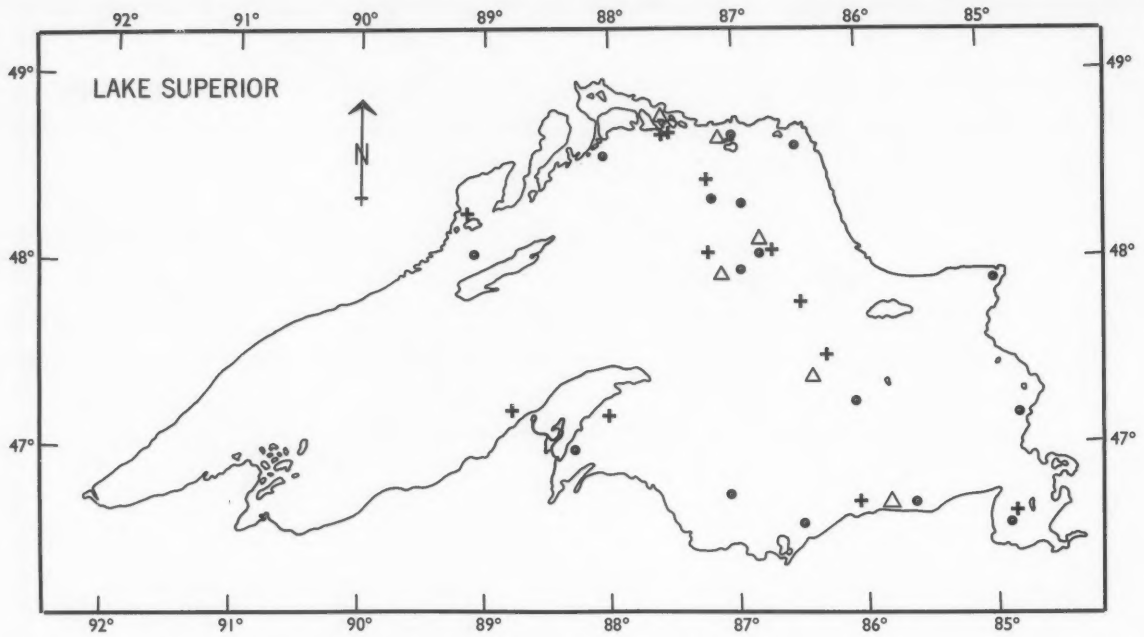


FIG. 1. Location of stations. ●, May; +, July; △, October.

However, the "low-light" cells had higher cellular phosphorus content than the "high-light" cells. Also, in several marine environments, maximal stimulation occurred in apparently phosphorus-sufficient populations which also had physiological symptoms of light limitation (Nalewajko and Lee 1983) and which were in an environment where a low-light regime was likely to prevail. The relative importance of the phosphorus status and the light history of a population to the extent of light stimulation thus remains unknown, and led us to undertake this investigation. A phosphate uptake system capable of responding positively to light intensity, particularly in a phosphorus- or light-limited environment, may offer the alga a competitive advantage over bacteria, and over species of algae not in possession of such ability.

Lake Superior was chosen as the study site because our earlier work (Nalewajko et al. 1981) led to unexpected conclusions on the light environment. In spite of the deep photic zone, the phytoplankton characteristics were consistent with periodic light limitation, which could be a result of the great depth of the lake, long periods without thermal stratification, and frequency of inclement weather. Our results on the phosphorus status of the lake were also intriguing, as they did not indicate the severe phosphorus limitation that might be expected in an oligotrophic lake.

Here we test the hypothesis that both light history and phosphorus status affect the response of phosphate uptake rate to irradiance. Solar radiation in the previous 3 d was selected as an estimate of light history because this appears to be an appropriate time scale for the occurrence of light adaptation in phytoplankton (Platt and Jassby 1976). Turnover time of phosphate was chosen as an index of the phosphorus status of the planktonic microorganisms (Lean and Nalewajko 1979). We chose to examine inshore and offshore areas of Lake Superior because these differ both in the duration of the stratified period (Bennett 1978), which would affect the light regime experienced by the phytoplankton, and in the phosphate turnover time, which suggests a difference in the phosphorus status (Shear et al. 1981).

Methods

The effects of light intensity on phosphate uptake were investigated on 34 occasions during five cruises on Lake Superior between May 1980 and July 1981. Station locations are shown in Fig. 1, and sampling frequency is given in Table 1. Stations <5 km and >5 km from shore were designated as inshore and offshore, respectively. This designation is supported by significant differences in water depth (Table 2) and is consistent with the subdivision into five inshore and one offshore region proposed by Munawar and Munawar (1978).

During periods of isothermal mixing, lake water samples for experiments were taken from 5 m using standard Van Dorn bottles, but when the lake was thermally stratified, integrated 0.5- to 10-m samples were used instead.

Prior to use, all glassware was washed in dilute H_2SO_4 (about 250 mmol·L^{-1}), rinsed well with distilled, deionised water, and dried at 105°C.

Rate constants of phosphate uptake were measured using carrier-free ^{32}P-PO_4 as described by Lean and Nalewajko (1979). The isotope was added immediately after the samples were collected. Experiments on phosphate uptake as a function of irradiance were carried out in the dark and at five light intensities in the 89−530 $\mu E \cdot m^{-2} \cdot s^{-1}$ range. The samples were kept at ambient lake water temperature in an incubator illuminated by high-output fluorescent lights (Canadian General Electric, F48PG17/CW). In all ^{32}P-PO_4 uptake experiments, 25- or 40-mL aliquots were filtered periodically over 1.5−3.0 h on

TABLE 1. Phosphate uptake as a function of light intensity, Lake Superior. DPTT, phosphate turnover time measured in the dark; an asterisk indicates PERL (the extreme response of phosphate uptake to light intensity <500 $\mu E \cdot m^{-2} \cdot s^{-1}$ as % of dark uptake).

Station	Depth (m)	Time of day	Inshore or offshore	Phytoplankton biovolume (10^6 µm)	DPTT (h)	Sunshine hours in previous 3 d	Rate constant of $^{32}P\text{-}PO_4$ uptake as % of dark uptake at light intensity ($\mu E \cdot m^{-2} \cdot s^{-1}$): 89	139	218	340	530
May 1980											
16	60	10:00	i	109.5	1.03	9.5	161.8*	134.6	129.2	126.6	126.0
18	82	07:30	i	—	1.78	9.0	99.6	94.5	91.2	75.6*	—
19	90	14:00	i	103.6	5.3	13.5	158.8	165.3	170.7	181.1*	169.7
20	102	19:00	i	190.9	3.8	22.1	115.3	117.2	—	120.9*	91.2
21	180	07:00	o	136.6	11.2	14.8	98.9	96.0	—	82.9	71.4*
21A	280	19:00	o	—	18.9	39.6	80.0	80.0	70.9*	80.0	83.4
22	210	07:00	o	383.0	18.0	35.3	103.7	101.4	81.0	78.8*	89.2
23	277	19:40	o	106.1	16.7	30.4	59.9	—	67.7	54.9	31.9*
May 1981											
12.1	140	08:00	i	408.4	5.3	9.7	127.7	151.9	161.0*	121.3	130.3
13.2	168	03:00	i	114.3	6.5	5.0	129.3*	111.3	104.3	108.6	—
14.1	217	10:00	o	79.7	23.5	12.7	—	91.7*	95.3	96.5	94.1
16	72	13:00	i	109.5	25.1	27.0	105.3	—	126.8*	109.3	84.0
17	55	19:00	i	169.1	2.6	32.3	98.1	89.8*	—	93.2	91.0
18	137	07:00	i	163.7	1.8	32.3	101.5	98.8	91.4	82.0*	—
19	220	13:00	i	—	9.0	35.7	93.5	88.4	87.0	80.0*	—
20	212	21:00	o	150.4	6.3	15.0	97.2	94.4*	94.5	96.6	95.1
July 1980											
10	140	15:00	i	233.1	0.49	18.7	126.1	147.4*	131.9	112.8	110.6
13	78	11:00	i	252.9	0.38	24.4	127.3	124.2	127.3	127.8	131.9*
18	23	11:00	i	320.8	0.28	29.7	136.4*	115.0	99.4	87.0	93.0
20	38	13:00	i	176.7	0.92	28.6	100.0	117.7	106.9	118.4*	94.9
21	52	18:00	i	234.0	0.28	30.6	98.1	101.0	103.1	109.5	110.0*
21A	140	00:30	i	221.7	0.53	31.1	113.7	107.2	118.9	128.1*	125.8
22	220	04:30	o	135.0	0.40	31.1	110.0*	99.0	97.8	101.2	96.9
23	180	07:40	o	162.0	0.92	31.3	97.2	100.3	104.7	107.5	110.0*
23A	100	12:00	o	312.5	1.1	32.9	115.2	125.3	138.0*	112.4	117.2
July 1981											
13B	26	00:10	i	305.2	0.34	19.3	125.0*	111.5	107.1	111.2	103.2
19	218	18:00	o	140.4	8.1	23.2	—	120.5	121.2*	116.1	117.4
21	255	18:00	o	—	23.3	27.1	110.9*	106.4	110.1	106.8	100.3
October 1980											
1	14	18:00	i	360.2	5.3	3.3	130.8*	127.1	122.7	127.4	112.0
2	219	18:00	o	—	10.2	1.5	103.5	89.7	81.6*	86.5	89.3
3	218	11:00	o	103.9	7.6	3.6	133.1	123.5	132.5	145.0*	125.7
4	152	15:00	i	—	3.6	5.0	107.4	105.1	120.9*	105.5	107.4
5	38	09:00	i	—	5.1	5.2	81.3	89.1	84.5	75.0*	77.6
7	219	08:00	o	206.9	4.4	4.4	101.2	85.9*	81.6	94.2	92.4

0.45-µm pore-size Sartorius cellulose acetate filters. In size fractionation experiments, 0.2- and 1-µm pore-size Nuclepore filters were used instead. The filters were rinsed twice with filtered lake water and placed in scintillation vials. Fifteen millilitres of PCS liquid scintillation solution (Amersham Corp.) was added to the wet filters and radioactivity was measured in a Beckman 230 scintillation counter.

In $^{32}P\text{-}PO_4$ experiments the initial slope of the curve obtained when ln % radioactivity remaining in filtrates is plotted against time represents k, the rate constant of radioisotope uptake. The slopes were calculated by linear regression. The reciprocal of k gives the turnover time of the external phosphate pool.

In experiments on the effects of irradiance on phosphate uptake, Student's t-test was applied to determine if the rate constant at a given irradiance was significantly different ($P \leq 0.05$) from the dark value. In the majority of cases a 10% difference proved to be not significant. The rate constant, at irradiances <500 $\mu E \cdot m^{-2} \cdot s^{-1}$, that differed most from the dark value was designated PERL, the extreme response of phosphate uptake to light intensity.

Chemical analyses and chlorophyll determinations were carried out at the Water Quality Branch Laboratory, Canada Centre for Inland Waters, (Environment Canada 1979) using standard procedures. Data on hours of sunshine were obtained from the Atmospheric and Environmental Services, Environment Canada. Phytoplankton enumerations were carried out

TABLE 2. Variables for Lake Superior, May 1980 – October 1981. Data are arranged by (A) inshore (<5 km from shore) and offshore stations and (B) season. Values shown are means. Within A and B groupings, Duncan's multiple range tests were used to identify values significantly different at $P < 0.05$ (underscored with a solid or broken line).

	A		B		
	Inshore	Offshore	May–June	July	October
PERL[a]	121.6	95.8	101.3	122.9	106.5
DPTT[b]	3.7	12.0	9.3	2.9	8.8
Temperature (°C)	7.9	5.0	3.0	10.9	6.6
Sunshine hours in previous 3 d	19.6	20.3	21.2	27.6	7.4
Total phosphorus ($\mu g \cdot L^{-1}$)	4.55	3.64	4.0	4.19	4.4
Depth (m)	81.1	206.2	156.4	116.5	118.5
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	0.98	0.74	1.20	0.88	0.56
Phytoplankton bio-volume ($10^6\ \mu m^3 \cdot L^{-1}$)	210.2	174.2	171.1	217.4	223.4
n in data set	20	14	16	12	6
Time of day			11:25	09:10	13:10

[a]PERL: extreme response of phosphate uptake to light intensity <500 $\mu E \cdot m^{-2} \cdot s^{-1}$ as % of dark uptake.
[b]DPTT: phosphate turnover time (h) measured in the dark.

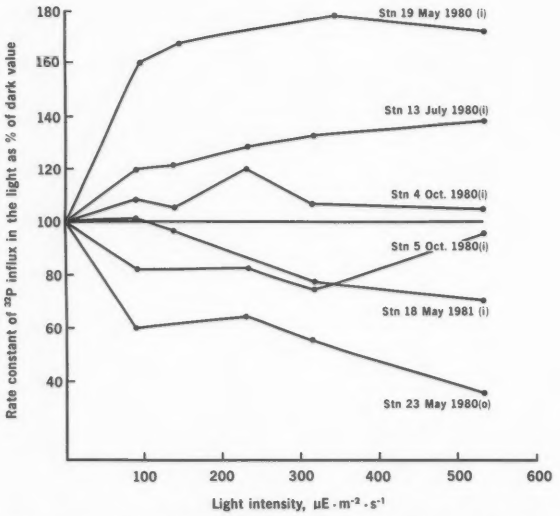


FIG. 2. Examples of phosphate uptake in the light (as % of dark value) as a function of light intensity. i = inshore stations, o = offshore stations.

according to the Utermohl method using a Wild Leitz inverted microscope and are reported in detail in Nalewajko and Voltolina (1986).

Results

In 17 of the 34 experiments, light significantly stimulated phosphate uptake above dark values, in 7 it had no significant effect, and in 10, significant inhibition ($P < 0.01$) was apparent at <500 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Table 1; Fig. 2). In the stimulated group, initial stimulation was commonly followed by lesser stimulation or inhibition at irradiances >500 $\mu E \cdot m^{-2} \cdot s^{-1}$.

TABLE 3. Stepwise multiple regression of PERL (extreme response of phosphate uptake to irradiance < 500 $\mu E \cdot m^{-2} \cdot s^{-1}$ as % of dark uptake) and four variables. PERL = −1.81 Sun 3d − 1.78 DPTT + 0.08 Phyto − 0.07 TMDAY.

Step	Variable	% of variance explained
1	Hours of sunshine in previous 3 d (Sun 3d)	20.3
2	Phosphate turnover time (h) measured in the dark (DPTT)	17.6
3	Phytoplankton biovolume (μm^3) (Phyto)	4.2
4	Time of day (TMDAY)	0.1
	Total variance explained by model	42.2

In Table 2, PERL and other variables have been segregated by location into inshore or offshore groups, and by season. In this format, mean PERL values did not differ significantly among seasons, but values inshore were significantly higher than offshore. Depth offshore was significantly greater, and phosphate turnover time measured in the dark (DPTT) was significantly longer than inshore.

A stepwise multiple regression analysis was carried out to rank the contribution of four variables to the variance of PERL (Table 3): in addition to hours of sunshine in the previous 3 d (Sun 3d) and DPTT, these included phytoplankton biovolume and time of day at which the phosphate uptake experiment was carried out. These variables were not significantly correlated

TABLE 4. Phosphate uptake in Lake Superior organisms <1 μm as % of total uptake (organisms >0.2 μm) at ambient temperature and 217 $\mu E \cdot m^{-2} \cdot s^{-1}$.

Station	Date	Location	Ambient temp. (°C)	(^{32}P-PO_4 in <1 μm)/(^{32}P-PO_4 in >0.2 μm) × 100 (%)
13	May 26, 1981	Inshore	7	70.9
14.1	May 27, 1981	Offshore	2.6	45
13B	July 21, 1981	Inshore	13.9	81.8
19	July 22, 1981	Offshore	5.6	43.3
21	July 21, 1981	Offshore	4.5	35.5

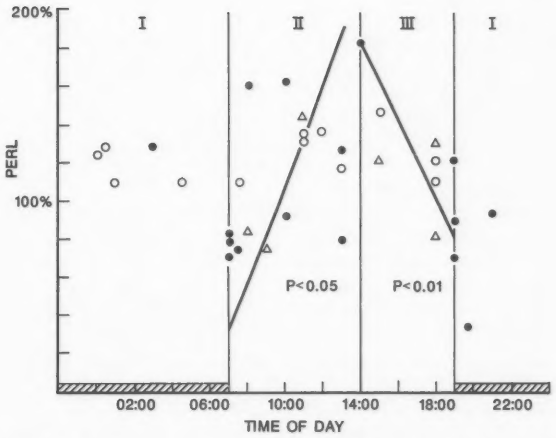


FIG. 3. PERL (extreme response of phosphate uptake to light intensity <500 $\mu E \cdot m^{-2} \cdot s^{-1}$) as a function of time of day. I, Sunset to sunrise; II, sunrise to maximal solar radiation, 14:00; III, 14:00 to sunset. In periods II and III, trend lines were drawn from linear regressions. ●, May–June; ○, July; △, October; hatched bars indicate night.

with each other. Time of day was included as a variable in view of an apparent diurnal pattern in the magnitude of stimulation of phosphate uptake by light (Fig. 3). Trends of PERL were examined in three time slots: I, night; II, period of increasing light intensity 07:00 to 14:00; III, period of decreasing light intensity 14:00 to 19:00. A significant ($P < 0.05$) trend of increasing PERL values was apparent in time slot II and decreasing values in time slot III. No significant linear trend was detected in PERL values measured during the night, but low values after sunset appear to be followed by higher values between 01:00 and 04:30, and low values occur again at sunrise.

The four-variable model (Table 3) explained 42.1% of the variance in PERL, with Sun 3d as the most important contributor, followed by DPTT. The contributions of phytoplankton biovolume and time of day were very small.

Size fractionation experiments at ambient temperature and 217 $\mu E \cdot m^{-2} \cdot s^{-1}$ indicated that lower proportions of ^{32}P-PO_4 uptake occurred in the <1 μm size fraction at the three offshore stations than at the two inshore stations (Table 4).

Discussion

Our data clearly demonstrate that phosphate uptake in Lake Superior is light sensitive, exhibiting stimulation or inhibition on more occasions than indifference. While the stimulation by light, observed in 17 of 34 experiments, amounted at most to 1.8 times the dark uptake the fact that it did occur in this oligotrophic lake negates the conclusions of Healey (1973), Lean and Pick (1981), and Perry (1976), among others, that stimulation is to be expected only when phosphate concentrations are high. However, the results are consistent with those from the Northern Sargasso Sea (Nalewajko and Lee 1983) where, in apparently phosphate-limited phytoplankton, light stimulated phosphate uptake to about 1.8 times the dark rate.

Here, the importance of light history to the stimulation or inhibition of phosphate uptake by light is apparent only indirectly from the emergence of Sun 3d as the most important variable in the stepwise multiple regression model of PERL. Further, any influence of past light regime may be confounded by the apparent diurnal pattern of the light effect on phosphate uptake. In the model, Sun 3d has a negative influence on PERL but the diurnal oscillations of PERL are characterized by highest values during daylight hours, while inhibition appears to be most common around sunrise and sunset.

Diel rhythms of phosphate uptake rates have been detected in natural populations of phytoplankton (e.g. Stross and Pemrick 1974), but were not present in Lake Superior during this investigation. Diel periodicity in the effect of light on phosphate uptake has not been investigated, and to our best knowledge, only one report (Lemasson et al. 1980) hints at its existence. These researchers, working in brackish, tropical waters which were not limited by phosphorus, reported a decreasing influence of light on phosphate uptake in four consecutive experiments from 07:00 to midnight.

Our discovery of a diel pattern in PERL was accidental. The fact that a posteriori analysis of data from experiments carried out at different seasons over a 17-mo study period still revealed a pattern suggests that it is strong and seasonally persistent. However, this diel pattern appears less important to variance of PERL than the light regime in the previous 3 d, according to the results of the stepwise multiple regression. The negative influence of Sun 3d on PERL means that light stimulation of phosphate uptake would be expected to increase as the light received in the previous 3 d decreased, and validates our hypothesis that phosphate uptake in phytoplankton from a low-light environment would show more pronounced stimulation by light.

Although Sun 3d was ranked as the most important variable in the PERL model, the phosphorus status of the population as estimated by phosphate turnover time was a close second. However, according to the model, PERL is higher when phosphate turnover time is shorter (Table 3). Also, PERL is significantly higher and phosphate turnover time significantly shorter inshore than offshore (Table 2). It appears, then, that light stimulates phosphate uptake more in the relatively more

phosphorus-stressed inshore areas, which is the reverse of the expected result (Cembella et al. 1984; Lean and Pick 1981).

Accurate assessment of the phosphorus status of microbial populations is difficult at best. We have used phosphate turnover time as an indicator (Lean and Nalewajko 1979), since recent evidence (Nalewajko and Voltolina 1986) suggests that it corresponds to the P_{max}/V_{max} ratio of Lean and Pick (1981). Both these indices show that offshore areas of Lake Superior are less stressed for phosphorus than inshore, even though in the latter the shortest phosphate turnover time observed was about 18 min, and the biphasic $^{32}P\text{-}PO_4$ uptake curve, typical in lakes at times of extreme phosphorus deficiency, was not observed (Lean and Nalewajko 1979; Shear et al. 1981). In the present context the establishment of an accurate phosphorus status for Lake Superior is less relevant than the fact that offshore areas appear to be relatively less stressed for phosphorus than inshore. Such a situation would arise if light intensity is the primary limiting factor for phytoplankton growth offshore but not inshore, as suggested by Nalewajko and Voltolina (1986). Cellular composition, including phosphorus content, responds differently to light and phosphorus limitation (Riegman 1985). According to Zevenboom (1980), Rhee and Gotham (1981), and Healey (1985), a light-limited culture growing at the same rate as a nutrient-limited culture would be characterized by a higher cell quota of the nutrient in question. The influx of $^{32}P\text{-}PO_4$ into a cell decreases as the cell phosphorus content increases; thus, phosphate turnover time becomes longer (Nalewajko and Lean 1978). We are hypothesizing that phytoplankton growth in the deep ($\bar{z}$ = 206.2 m, Table 2) offshore waters which are thermally stratified for only about 5 mo, is primarily limited by light, leading to a shortage of carbon relative to phosphorus in the cells. These cells, if light limitation is extreme, may sacrifice phosphate uptake for photosynthetic carbon fixation when exposed to light, so that phosphate uptake in the light decreases to a fraction of the dark value. Inhibition of phosphate uptake at even the lowest light intensities was most common offshore (Tables 1 and 2), but also occurred inshore in May and October (Table 1), and appears to be more common around sunrise and after sunset (Fig. 3). It is thus consistent with our hypothesis that deep mixing could induce a state of extreme light limitation in the phytoplankton but suggests further that several hours of darkness may have a similar effect.

However, we are puzzled why in low-light *Chlorella*, phosphate uptake was greatly stimulated by light (Nalewajko and Lee 1983). Possibly the degree of light limitation is important, through its effect on the relative sizes of various cellular components such as carbohydrates, proteins, ATP, and phosphorus as well. Growth rate of the *Chlorella* was limited by low light to about half the rate in high light. We used axenic *Chlorella* cultures in our experiments (Nalewajko et al. 1981), but are dealing with mixed algal and bacterial populations in lake water. In Lake Superior the use of a 1-μm pore size filter to distinguish between algae (>1 μm) and bacteria (<1 μm) proved impossible. The <1 μm size fraction contains picoplankton as well as bacteria. The picoplankton showed symptoms of low light adaptation. Light saturation of photosynthesis occurred at lower intensities than in the larger algae and inhibition set in at about 250 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Nalewajko and Voltolina 1986). Since phosphate uptake shows light saturation and inhibition at lower light intensities than photosynthesis (Nalewajko and Lee 1983), we suggest that phosphate uptake in picoplankton may be already inhibited at 89 $\mu E \cdot m^{-2} \cdot s^{-1}$, the lowest light intensities used in most of our experiments. Planas (1978) showed that photphate uptake in a bacterial culture decreased as a function of light intensity up to 250 $\mu E \cdot m^{-2} \cdot s^{-1}$; thus, it is not possible to conclusively attribute the observed inhibition of uptake either to picoplankton or bacteria. The proportion of phosphate uptake occurring in the <1 μm size fraction was higher inshore than offshore (Table 4), but we have no data on the abundance of bacteria in these experiments.

We propose that phosphate uptake will increase moderately with increasing light intensity if phytoplankton growth is not limited by light and moderately limited by phosphorus. Such a situation would be analogous to the high-light *Chlorella* in which PERL was about 130% (Nalewajko et al. 1981), and may be representative of, for example, inshore areas of Lake Superior (Table 2). These explanations do not preclude the occurrence of maximal PERL values in light limited phytoplankton under conditions which permit luxury phosphorus uptake to occur. Neutral responses would occur if phytoplankton was light and phosphorus limited, or not limited by either but not phosphorus rich.

The hypothesis that light history and phosphorus status are both involved in controling the response to light needs further experimental verification. At present we cannot discard the possibility that both sunshine in the previous 3 d and the time of day affect PERL simply via changes in cellular phosphorus content, or the possibility that temperature, which also affects cellular phosphorus quotas, is involved (Rhee and Gotham 1981). An interesting question is whether C:P ratios are important to this phenomenon, and whether the mechanism involves a C:P-dependent competition for ATP between carbon fixation and phosphate uptake. The nature of the diel pattern in the response of phosphate uptake to light is intriguing, as is its phase relative to the apparent diel pattern of assimilation numbers (Nalewajko and Voltolina 1986) in Lake Superior.

Acknowledgements

Funds for this research were provided by an NSERC operating grant to the senior author. We thank L. Pavone and C. Ewing for assistance with the computer analyses and Dr. D. Voltolina for comments on the revised manuscript.

References

BENNETT, E. B. 1978. Characteristics of the thermal regime of Lake Superior. J. Great Lakes Res. 4: 310–319.

CEMBELLA, A. D., N. J. ANTIA, AND P. J. HARRISON. 1984. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective: Part 1. Rev. Microbiol. 10: 317–391.

ENVIRONMENTAL CANADA. 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

HEALEY, F. P. 1973. Inorganic nutrient uptake and deficiency in algae. Crit. Rev. Microbiol. 3: 69–113.

1985. Interacting effects of light and nutrient limitation on the growth rate of *Synechococcus linearis* (Cyanophyceae). J. Phycol. 21: 134–146.

KUENZLER, E. J., D. W. STANLEY, AND J. P. KOENINGS. 1979. Nutrient kinetics of phytoplankton in the Pamlico River, North Carolina. Rep. No. 139, Water Research Institute of the University of North Carolina.

LEAN, D. R. S., AND C. NALEWAJKO. 1979. Phosphorus turnover time and phosphorus demand in large and small lakes. Arch. Hydrobiol. Beih. Ergel 13: 120–132.

LEAN, D. R. S., AND F. R. PICK. 1981. Photosynthetic response of lake plankton to nutrient enrichment: a test for nutrient limitation. Limnol. Oceanogr. 26: 1001–1019.

LEMASSON, L., Y. PAGES, AND Y-L. CREMOUX. 1980. Inorganic phosphate uptake in a brackish tropical lagoon. Estuarine Coastal Mar. Sci. 11: 547–561.

MUNAWAR, M., AND I. F. MUNAWAR. 1978. Phytoplankton of Lake Superior, 1973. J. Great Lakes Res. 4: 415–442.

NALEWAJKO, C., AND C. GARSIDE. 1983. Methodological problems in the simultaneous assessment of photosynthesis and nutrient uptake in phytoplankton as function of light intensity and cell size. Limnol. Oceanogr. 28: 591–597.

NALEWAJKO, C., AND D. R. S. LEAN. 1978. Phosphorus kinetics – algal growth relationships in batch cultures. Mitt. Int. Ver. Theor. Angew. Limnol. 21: 184–192.

NALEWAJKO, C., AND K. LEE. 1983. Light stimulation of phosphate-uptake in marine phytoplankton. Mar. Biol. 74: 9–15.

NALEWAJKO, C., K. LEE, AND H. SHEAR. 1981. Phosphorus kinetics in Lake Superior: light intensity and phosphate uptake in algae. Can. J. Fish. Aquat. Sci. 38: 224–232.

NALEWAJKO, C., AND D. VOLTOLINA. 1986. Phytoplankton, assimilation numbers and environmental variables in Lake Superior. Can. J. Fish. Aquat. Sci. 43. (In press).

PERRY, J. J. 1976. Phosphate utilization by an oceanic diatom in phosphorus limited chaemostat culture and in the oligotrophic waters of the central North Pacific. Limnol. Oceanogr. 21: 88–107.

PLANAS, D. 1978. Phosphorus uptake rates in planktonic communities related to light gradient. Int. Ver. Theor. Angew. Limnol. Verh. 20: 2731–2736.

PLATT, T., AND A. D. JASSBY. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. 12: 421–430.

RHEE, G-Y., AND I. J. GOTHAM. 1981. The effect of environmental factors on phytoplankton growth: light and the interactions of light with nitrate limitation. Limnol. Oceanogr. 26: 649–659.

RIEGMAN, R. 1985. Phosphate–phytoplankton interactions. Doctoral thesis, University of Amsterdam, Amsterdam, The Netherlands. 143 p.

RIVKIN, R. B., AND E. SWIFT. 1982. Phosphate uptake by the dinoflagellate *Pyrocystis noctiluca*. J. Phycol. 18: 113–120.

SHEAR, H., K. LEE, AND C. NALEWAJKO. 1981. A seasonal survey of phosphorus kinetics in Great Lakes phytoplankton. Poster, 44th Annual Meeting, American Society of Limnology and Oceanography, Milwaukee, WI.

STROSS, R. G., AND S. M. PEMRICK. 1974. Nutrient uptake in phytoplankton: a basis for niche separation. J. Phycol. 10: 164–169.

ZEVENBOOM, W. 1980. Growth and nutrient uptake kinetics of *Oscillatoria agarahii*. Doctoral thesis, University of Amsterdam, Amsterdam, The Netherlands. 178 p.

Microbial Recycling of Phytoplankton Phosphorus[1,2]

Joseph V. De Pinto,[3] Thomas C. Young, James S. Bonner,[4] and Paul W. Rodgers[5]

Department of Civil and Environmental Engineering, Clarkson University, Potsdam, NY 13676, USA

De Pinto, J. V., T. C. Young, J. S. Bonner, and P. W. Rodgers. 1986. Microbial recycling of phytoplankton phosphorus. Can. J. Fish. Aquat. Sci. 43: 336–342.

The remineralization of phytoplankton-bound phosphorus subsequent to nonpredatory phytoplankton mortality represents a significant source of algal-available phosphorus in many lakes. A unique experimental apparatus (A Dual Culture Diffusion Apparatus) was used to measure the rate and extent of this process and to elucidate some of the governing factors. It was demonstrated that this process is strongly influenced by heterotrophic decomposer activity, because phosphorus regeneration rates were less than 0.01/d for cultures not inoculated with a decomposer community, while they were two to five times higher for decomposer-inoculated cultures. In addition to the character and activity of the microbial decomposer community, the phytoplankton cell phosphorus content was shown to be a significant factor in the rate of phosphorus regeneration for a given cell decay rate. Cell phosphorus above the minimum cell quota appeared to be released in an available form quite rapidly upon algal death and lysis.

Dans bon nombre de lacs, la reminéralisation du phosphore phytoplanctonique, suite à la mort (autre que par prédation) du phytoplancton, représente une source appréciable de phosphore pouvant être assimilé par les algues. Un dispositif expérimental spécial (un appareil à diffusion pour double culture) a servi à déterminer le taux et l'étendue de ce processus et à découvrir certains des facteurs le régissant. Il a été montré que ce phénomène dépendait fortement de l'activité des décomposeurs hétérotrophes car les taux de régénération du phosphore étaient inférieurs à 0,01/jour dans les cultures n'ayant pas été inoculées avec une communauté de décomposeurs, tandis qu'ils étaient de deux à cinq fois supérieurs dans les cultures inoculées. En plus de dépendre du type et de l'activité de la communauté microbienne de décomposeurs, la teneur cellulaire en phosphore du phytoplancton avait un effet appréciable sur le taux de régénération du phosphore, ceci à un taux donné de décomposition cellulaire. Le phosphore cellulaire qui ne fait pas partie de la structure cellulaire de base est assez rapidement libéré sous une forme assimilable après la mort et la lyse de l'algue.

Received November 2, 1984
Accepted May 17, 1985
(J8001)

Reçu le 2 novembre 1984
Accepté le 17 mai 1985

The importance of phosphorus recycling in lakes is well established. There are several examples of lake systems that maintain a significant standing crop of phytoplankton long after the major spring influx of available phosphorus has been converted to biomass (Larson et al. 1973; DiToro and Connolly 1980; Gulliver and Stefan 1982). Without significant phosphorus recycling in these systems, the various plankton loss processes would rapidly deplete the available pool of this often-limiting nutrient, thus precluding mid- and late-summer blooms.

One of the more significant phosphorus recycle processes in lakes is the remineralization of phytoplankton-bound phosphorus upon algal death and decomposition (Charlton 1975; Bloesch et al. 1977; De Pinto and Verhoff 1977; Fallon and Brock 1979). The purpose of this study was to investigate the effect of certain environmental factors on the rate of algal-available phosphorus recycling due to nonpredatory phytoplankton mortality.

Conceptual Model of Bioavailable Phosphorus Sources in Lakes

The pool of algal-available phosphorus in lakes can be replenished by a number of different means. A conceptualization of the processes that represent a source of phosphorus to this pool is presented in Fig. 1.

The major difference between this model and most current phytoplankton models is the distinction between allochthonous and autochthonous ultimately available phosphorus compartments. Performing separate mass balances on these two unavailable phosphorus compartments is necessitated by the experimentally determined differences in their transport characteristics and in their rate and extent of conversion to algal-available phosphorus (De Pinto et al. 1981; Martin et al. 1984).

Internal phosphorus recycling is defined herein as the conversion of autochthonous unavailable phosphorus, primarily biotically bound, to an available form that can be taken up and

[1]This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock Univeristy, St. Catharines, Ont., May 1984.

[2]Although the research described in this article has been funded wholly or in part by the U.S. Environmental Protection Agency, it has not been subjected to the Agency's required peer and policy review and, therefore, does not necessarily reflect the views of the Agency and no official endorsement should be inferred.

[3]Author to whom correspondence should be addressed.

[4]Current address: Center for Earth and Environmental Science, SUNY-Plattsburgh, Plattsburg, NY 12901, USA.

[5]Current address: Limno-Tech, Inc., Ann Arbor, MI 48103, USA.

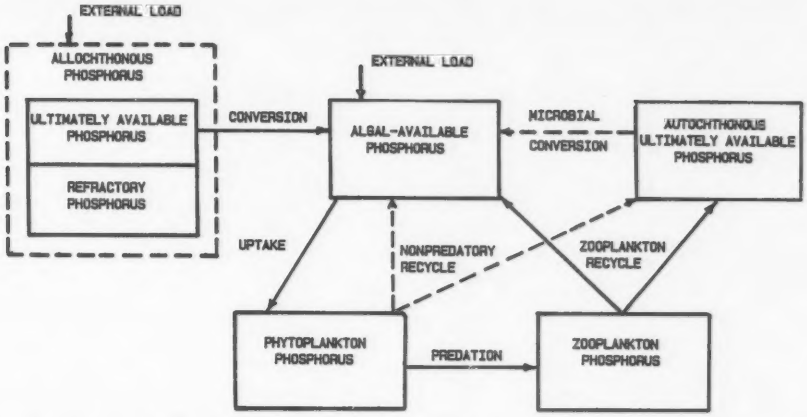


FIG. 1. Conceptual model of the processes that generate algal-available phosphorus in a lake water column shows the part that nonpredatory phytoplankton mortality plays in phosphorus recycling. Broken lines indicate pathways investigated in this study.

utilized by phytoplankton. As shown, the two major water column recycle processes are nonpredatory recycle from phytoplankton and zooplankton recycle. They can contribute directly and/or indirectly to the algal-available phosphorus pool and are described as follows: (1) zooplankton grazing of phytoplankton and phosphorus-containing detritus, followed by excretion of available and unavailable forms and (2) phosphorus released in an available or unavailable form by phytoplankton excretion or by cell lysis due to nonpredatory mortality, followed by transformation of the unavailable form (either soluble organic phosphorus or cell residue) to algal-available phosphorus by microbial-induced mineralization.

Internal phosphorus, which is positionally unavailable because it is below the euphotic zone in the lower hypolimnion or bottom sediments, can become available through various physical and/or biochemical processes. Examples include bottom sediment release of orthophosphate due to diffusion or bioturbation, sediment resuspension and subsequent available phosphorus release from the particulates, and phosphorus transport up or down in the water column due to zooplankton migration. Bottom sediment phosphorus is composed of both allochthonous and autochthonous forms, although both forms may have been modified by residence in the benthic environment. Evidence exists that, in terms of rate and extent of available phosphorus release, resuspended bottom sediments exhibit an intermediate behavior between external tributary solids and decomposing algal biomass (Martin et al. 1984; Young and De Pinto 1982).

Experimental Approach

Dual Culture Diffusion Apparatus

The process experimental apparatus we used is one that was designed to measure, in an unambiguous manner, the phosphorus that could be considered truly available on the basis of uptake by a test organism during exposure to particulate-bound phosphorus as its only source. Design and operational details of the Dual Culture Diffusion Apparatus (DCDA) utilized for the bioassays can be found in De Pinto (1982); however, a brief description of the method is presented here.

The DCDA was employed in this study to directly determine the rate and extent of release of algal-available phosphorus by a stressed algal culture undergoing nonpredatory death and decay. This measurement was accomplished by placing a phosphorus-starved "assay" culture on one side of this two-chambered, continuous-medium vessel with the other side containing the "regeneration" algal culture. The regeneration culture, being darkened and in some cases inoculated with a decomposer community collected from an actual lake system, would then release phosphorus at a certain rate. The algal-available phosphorus released on the regeneration side of the DCDA could then diffuse across the 0.4-μm membrane separating the two cultures to the assay side, where the phosphorus-starved assay culture would rapidly immobilize the available phosphorus. Periodic harvesting of the assay culture to measure its accumulation of available phosphorus provided, therefore, a direct measure of the rate and cumulative amount of bioavailable phosphorus released from the decaying algae on the regeneration side of the DCDA.

Procedures and Data Analysis

The test algal culture that was placed in the darkened regeneration side of the DCDA was developed by inoculation of the test algal species into a growth medium consisting of nutrient-spiked Lake Ontario water collected from the water intake at Sackets Harbor, New York. The growth medium was prepared by amending the lake water with micronutrients in the levels recommended for the synthetic freshwater medium "WC" of Guillard and Lorenzen (1972), with nitrate–nitrogen at a 40:1 N/P gram-atomic ratio to insure phosphorus limitation, and with phosphorus at a level that would provide for a desired biomass and phosphorus cell content after a fixed batch growth period. This spiked lake water was then filter-sterilized by pressure filtration through 0.2-μm membrane filters and inoculated with a bacteria-free experimental phytoplankton stock culture. After a designated growth period, the culture was dispensed into the dark side of a preautoclaved DCDA. An aliquot of the culture was analyzed at this time to determine initial biomass and phosphorus content of this regeneration culture. Next, depending on the desired experimental conditions, a decom-

TABLE 1. Summary of results on phytoplankton cell volume decay and phosphorus regeneration (mean ± SE). Data demonstrate the effect of a decomposer community inoculum on both rates.

Species	No. of cultures	Decomposition conditions	Cell volume decay rate, $K_d(d^{-1})$	P regeneration rate $K_r(d^{-1})$
Scenedesmus	4	Uninoculated	0.022(±0.008)	0.005 (±0.002)
	7	Inoculated, young	0.039(±0.014)	0.023 (±0.014)
	5	Inoculated, old	0.057(±0.025)	0.0014(±0.0005)
	6	Inoculated, heat treatment	0.165(±0.051)	0.036 (±0.019)
Chlorella	1	Uninuculated	0.014	<0.001
	9	Inoculated	0.123(±0.032)	0.056 (±0.015)
Microcystis	4	Uninoculated	0.018(±0.02)	0.012 (±0.01)
	13	Inoculated	0.058(±0.028)	0.03 (±0.013)

poser inoculum was added to the regeneration vessel. Several control experiments were conducted, to which no decomposer inoculum was added, to measure the phosphorus release due to phytoplankton autolysis.

The decomposer inoculum was obtained from one of three lake systems: Lake Ozonia (New York), Lake Ontario (Sackets Harbor), and Stone Lake (Michigan), in order of least to most productive. A decomposer inoculum was isolated from a given lake water sample by passing the water through a 3.0-μm (or 20-μm in some cases) polycarbonate membrane filter, followed by collection of the particulates from this filtrate on a 0.2-μm filter. The decomposer organisms collected on the 0.2-μm filter were then concentrated in a small volume of filter-sterilized lake water for inoculation into the DCDA. Fresh lake water was used to obtain a decomposer inoculum for each DCDA run. This approach had the advantage of assuring a viable and realistic decomposer community, but had the disadvantage of introducing temporal variability into the community character and quantity.

In order to assure the rapid uptake of phosphorus diffusing across the membrane from the regeneration vessel into the assay vessel, a phosphorus-starved culture of *Scenedesmus* sp. (Rhee 1973) was kept in the assay vessel and replaced at 3- to 7-d intervals, depending on regeneration activity. The assay *Scenedesmus* culture was prepared by growing these algae in the same nutrient-amended Lake Ontario water as used on the dark side, except with a lower initial phosphorus level (25 μg P/L). Only 10- to 14-d-old cultures that had reached their peak biomass were used as assay cultures in the DCDA's. When a fresh assay culture was needed for the DCDA, both the harvested assay culture and an aliquot of the refill culture were analyzed for total particulate and total soluble phosphorus. All phosphorus measurements were performed using a colorimetric determination according to the single reagent method of Murphy and Riley (1962), preceded by an acid-persulfate digestion when required.

A kinetic analysis of experiments such as the one described was accomplished by performing a mass balance on phosphorus in both sides of the DCDA. Previous work (De Pinto et al. 1981; De Pinto 1982; Young et al. 1982) has indicated that the kinetics of release of available phosphorus from aquatic particulates are such that accumulation of phosphorus in the assay algae of the DCDA under bioassay conditions can be approximated by a first-order function of the amount of ultimately available phosphorus on the regeneration side. By combining this first-order release assumption with the definition that phosphorus taken up by the assay algae is available phosphorus and including the assumptions that there is no rate limitation by assay algae phosphorus uptake or by diffusion through the membrane (both of these rates have been shown to be rapid relative to phosphorus regeneration), the following equation has been developed as a description of the process (De Pinto 1982):

$$(1)\quad \mathrm{BAP}(t) = \mathrm{P}_0\,(1 - \exp(-k_r t))$$

where $\mathrm{BAP}(t)$ = cumulative available phosphorus released from the regeneration culture of algae during time t, P_0 = ultimate amount of available phosphorus that could be released from the regeneration culture over an arbitrarily long time period, and k_r = first-order coefficient for release of available phosphorus from the regeneration culture. Thus, the periodic harvesting and accumulated phosphorus measurement of the assay culture provided the data necessary to analyze phosphorus release from decaying algae in terms of a rate and ultimate extent — both measurements being essential coefficients in phytoplankton models.

Experimental Variables

As discussed previously, the primary objective of the DCDA experimentation was to measure the rate at which phosphorus is regenerated from phytoplankton decaying in a darkened environment. As a result, the following experimental variables were incorporated into this study: phytoplankton species used for the regeneration culture (*Scenedesmus* sp., *Chlorella vulgaris*, *Microcystis* sp.), the initial cellular phosphorus content of the regeneration culture at darkening, and the impact of the presence of a microbial decomposer community on algal decay and phosphorus regeneration.

Results

The results of 49 DCDA experiments (all run in triplicate) conducted on three phytoplankton species were analyzed to obtain first-order (base e) cell volume decay rates and phosphorus regeneration rates. A summary of these results is presented in Table 1, where the results have been averaged over inoculation conditions for a given species. For all three species the decomposer-inoculated cultures demonstrated more active decay and phosphorus regeneration, as a rule, than the uninoculated cultures. Uninoculated cultures, which are presumed to represent the result of only endogenous decay of the algae, typically exhibited cell volume decay rates of approximately 0.02/d, with phosphorus regeneration rates less than 0.01/d.

TABLE 2. Cell volume decay and phosphorus regeneration results for decomposer-inoculated *Scenedesmus* cultures. Data are arranged by culture conditions to show the effect of cell phosphorus content and decay rate on phosphorus regeneration rate. NA = not applicable.

Reactor	Cell P at darkening ($\mu g\ P/mm^3$)	Cell volume decay rate, $K_d(d^{-1})$	P regeneration rate, $K_r(d^{-1})$	Ratio K_r/K_d
		Live, young cultures[a]		
S.1	2.08	0.032	0.004	0.125
S.2	2.47	0.065	0.027	0.415
S.3	2.67	0.034	0.014	0.412
S.4	3.71	0.031	0.006	0.194
S.5	3.97	0.050	0.038	0.760
S.6	4.29	0.038	0.031	0.816
S.7	5.30	0.024	0.039	1.625
		Live, old cultures[b]		
S.8	0.94	0.043	0.002	0.047
S.9	1.64	0.074	0.001	0.014
S.10	1.91	0.090	0.001	0.011
S.11	2.20	0.027	0.001	0.037
S.12	2.40	0.052	0.002	0.038
		Heat-treated cultures[c]		
S.13	4.90	0.132	0.019	NA
S.14	5.04	0.214	0.014	NA
S.15	5.21	0.133	0.032	NA
S.16	10.90	0.160	0.035	NA
S.17	13.30	0.110	0.057	NA
S.18	16.70	0.240	0.059	NA

[a]Cultures 7 d old at start of dark incubation.
[b]Cultures 30 d old at start of dark incubation.
[c]Cultures heat treated at 80°C for 1 h prior to incubation.

Certainly the presence of a microbial decomposer community had a profound influence on the rate of cell decomposition and phosphorus regeneration.

Scenedesmus Cultures

The decomposer-inoculated *Scenedesmus* cultures can be placed into three broad categories based on culture age and decomposition conditions (see Table 1). Seven reactors contained young cultures that were darkened before reaching a stationary phase, while five other reactors contained relatively old cultures that had reached a growth plateau. The final six reactors contained young populations that were killed by mild heat treatment (80°C for 1 h) prior to initiating the DCDA incubations. These experiments demonstrated that for algae decaying in the presence of a decomposer community, both the cell phosphorus content and the decay rate of the algae play a role in governing the phosphorus regeneration rate. In terms of cell volume decay rates, the heat-treated cultures produced the highest values, followed by the scenescent cultures and finally by the younger cultures. This same trend, however, was not evident for the phosphorus regeneration rates, although the apparent discrepancy could be reconciled by examining the initial cell phosphorus content in conjunction with the decay rate.

The effect of initial cell phosphorus content and cell decay rate (K_d) on the phosphorus regeneration rate (K_r) can be seen by calculating the ratio K_r/K_d versus initial cellular phosphorus for all live, decomposer-inoculated *Scenedesmus* cultures (Table 2). By normalizing the data to K_d, which appears to be the rate-limiting step, a more valid relationship between K_r and initial cell phosphorus content can be observed. As illustrated in Table 2, cultures having a cellular phosphorus content close to the minimum cell quota, $\leq 2.5\ \mu g\ P/mm^3$, showed low phosphorus regeneration rates relative to the amount of cell decay. The lowest K_r/K_d ratios came exclusively from the old cultures, in which the extended growth period allowed time for most of the phosphorus to be assimilated by the cells, thus leaving very little excess stored cellular inorganic phosphorus at the start of the experiments. This low regeneration rate is, therefore, indicative of the stoichiometric regeneration of the more tightly bound organic cell phosphorus for a given amount of biomass decay. On the other hand, as the initial cell quota increased above the minimum, the cultures demonstrated an increasing K_r/K_d ratio (an increasing rate of phosphorus release for the amount of decay occurring). The explanation for this result lies in the inherently more rapid release of excess inorganic phosphorus in combination with the large amounts of this fraction in cultures with a higher cell quota.

The concept of phosphorus regeneration rate being governed by cell decay and phosphorus content is corroborated by the six *Scenedesmus* cultures that were heat-treated prior to dark incubation. The heat treatment had the effect of reducing rate limitation resulting from using live cells. Not only were the cell volume decay rates and phosphorus regeneration rates higher for these cultures, but K_r exhibited a reasonably good correlation with the initial cell phosphorus content ($r = 0.923$, $\alpha < 0.01$). Because higher cell phosphorus suggests more stored inorganic phosphorus and because the cell death step has been bypassed in these cultures, this result seems quite logical.

Chlorella Cultures

In order to evaluate the dependence of phosphorus regeneration on the source and character of the decomposer community, a series of experiments was run using the green alga *Chlorella vulgaris* for which the decomposer inoculum was the only experimental variable. All experimental cultures came from the same source culture and, consequently, were the same age and cell phosphorus content at the start of the DCDA experiments. Any observed differences in decay rates and phosphorus regeneration rates could, therefore, only be attributed to decomposer conditions.

A summary of the results of the *Chlorella* experimental series is presented in Table 3. All cultures except DCDA number C.1 received a decomposer inoculum from either hypereutrophic Stone Lake or mesotrophic Lake Ontario. As stated earlier, very little decay or phosphorus regeneration took place in the uninoculated culture; culture C.1 was still green and had experienced very little suspended solids decrease after 30 d of dark incubation.

The remaining cultures not only received decomposer inocula from the two sources as indicated but the inocula were size fractioned into particles either $<20\ \mu m$ or $<3\ \mu m$. Among the cultures given a $<20\ \mu m$ inoculum (C.2–C.6), the Stone Lake concentrates seemed to produce consistently higher cell volume decay rates with somewhat higher phosphorus regeneration rates. This trend, however, was not observed in the cultures receiving the $<3\ \mu m$ inoculum. Perhaps some protozoan in the Stone Lake concentrate may have caused the increased rate of cell lysis, although this hypothesis was not confirmed by microscopic examination of cultures.

Although the phosphorus regeneration rates in this exper-

TABLE 3. Cell volume decay and phosphorus regeneration rates for *Chlorella* cultures. This table shows that the source of decomposer inoculum can influence cell decay and phosphorus recycle.

Reactor	Decomposer conditions[a]	Cell P at darkening ($\mu g\ P/mm^3$)	Cell volume decay rate, $K_d(d^{-1})$	P regeneration rate, $K_r(d^{-1})$
C.1	Uninoculated	1.72	0.014	<0.001
C.2	SLW < 20 μm	1.81	0.15	0.079
C.3	SLW < 20 μm	1.85	0.14	0.065
C.4	SLW < 20 μm	1.65	0.14	0.070
C.5	LOW < 20 μm	1.84	0.080	0.064
C.6	LOW < 20 μm	1.62	0.090	0.060
C.7	5 × SLW < 3 μm	1.75	0.14	0.049
C.8	SLW < 3 μm	1.55	0.070	0.044
C.9	SLW < 3 μm	1.51	0.090	0.029
C.10	LOW < 3 μm	1.52	0.11	0.048

[a]For inoculated cultures, letters indicate source of decomposer inoculum (SLW = Stone Lake water; LOW = Lake Ontario water) and size parameter indicates filter pore size used to collect inoculum in filtrate.

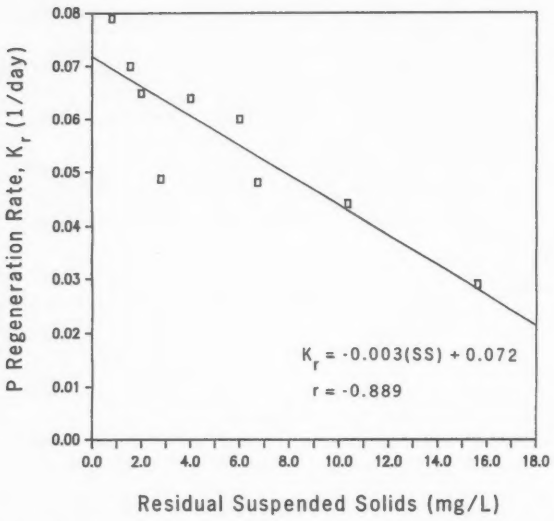


FIG. 2. Plot of phosphorus regeneration rate coefficient versus residual suspended solids after 30 d of dark incubation of decomposer-inoculated *Chlorella* cultures demonstrates the significance of detritus breakdown in the phosphorus regeneration process. Straight line represents a linear regression of data.

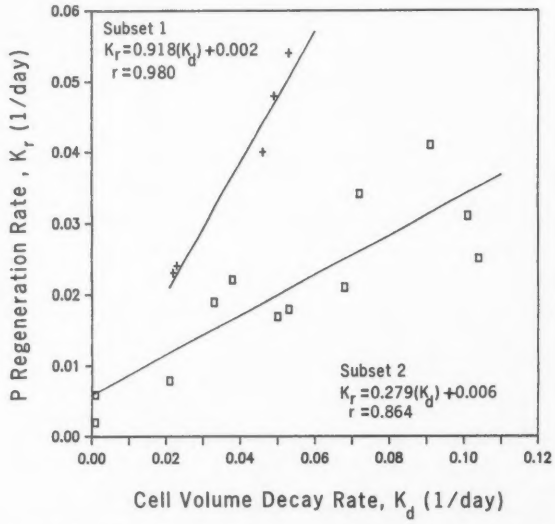


FIG. 3. Plot of phosphorus regeneration rate coefficient versus cell volume decay rate coefficient for all *Microcystis* cultures indicates that the relationship can vary seasonally, but in any event, phosphorus recycling by this process is closely correlated with phytoplankton decay. Straight lines represent linear regressions of two subsets of the data, differentiated by time of decomposer-inoculum collection from Lake Ontario.

imental series were somewhat correlated with cell volume decay rates, the most significant association we observed was between the phosphorus regeneration rates and the residual suspended solids after the 30-d dark incubation period. The excellent inverse relationship between K_r and residual suspended solids is demonstrated in Fig. 2. Thus, breakdown of detritus, in addition to algal death and lysis, is necessary for phosphorus regeneration.

Microcystis Cultures

A comparison of phosphorus regeneration between green algae and blue-greens was attempted by running a series of DCDA experiments with *Microcystis* sp. as the test organism. Several experiments were conducted with the decomposer inoculum taken from Lake Ontario in all cases, although at different times of the year.

Since all decomposer inocula came from Lake Ontario and since, with two exceptions, the initial cell phosphorus at darkening was not highly variable, one might expect good correlation between the cell volume decay rate (K_d) and the phosphorus regeneration rate (K_r). In Fig. 3, K_r is plotted versus K_d for all *Microcystis* cultures. Although a general trend is evident (linear correlation coefficient including all points is $r = 0.535$), there is certainly not a good correlation. An inter-

esting thing happens, however, if the correlation analysis is refined by subsetting the observations according to decomposer inocula. That is, 5 of the cultures from one run may be treated separately from the other 12 cultures, since these 5 cultures all received the same Lake Ontario inoculum, which was collected at a different time of the year (subset 1, September) than the other inocula (subset 2, March). Regressions on the two subsets taken separately yield very good correlations, as shown in Fig. 3.

Discussion

Our results point to some significant governing parameters for the process of nonpredatory algal death and subsequent phosphorus recycle and provide information useful for converting the conceptualization of this process into a deterministic description. We observed that the presence of a microbial decomposer community accelerated both decay of algae and the subsequent phosphorus mineralization. This finding confirms what has been reported in a number of previous studies of algal loss processes (Daft and Stewart 1973; Reim and Shane 1974; De Pinto and Verhoff 1977; Fallon and Brock 1979).

The conversion of algal biomass phosphorus to available phosphorus can be thought of deterministically as a two-step process: (1) algal death and lysis with the immediate release of stored excess inorganic phosphorus and (2) microbial mineralization of the remainder of the cell phosphorus to an available form. For the excess cell phosphorus the rate-limiting step appears to be cell death and lysis, while for the more tightly bound cell phosphorus the microbial mineralization step controls the overall conversion rate. This two-step conceptualization of the process is consistent with the variable-stoichiometry, internal nutrient pool theories experimentally supported by the work of Rhee (Rhee 1973, 1980) and field tested by the phytoplankton model of Bierman (Bierman et al. 1980; Bierman and Dolan 1981).

In addition to the physiological state of the algae, an important factor in the overall process of microbial phosphorus recycle is the character and activity of the microbial decomposer community. The results of the *Chlorella* experiments suggest that microbes isolated from more productive lake ecosystems have the potential to accelerate the process by increasing the decomposition rate. Rodgers and De Pinto (1983) also made the same observation in two-stage continuous flow experiments on decomposition of phytoplankton. DiToro and Matystik (1979) observed that a model with a genuine first-order phosphorus recycle mechanism could not account for the more rapid recycle rates required in higher trophic state Great Lakes. They therefore proposed a phosphorus recycle rate coefficient that was a saturating function of the system's chlorophyll level. This was an attempt to implicitly model the adaptation of the decomposers to high primary productivity.

From the *Microcystis* experiments we suggest that there is a seasonal adaptation by decomposers, probably in response to environmental factors, such as temperature, to phytoplankton community composition, and to increased phytoplankton biomass during blooms. In attempting to apply Bierman's multiclass phytoplankton model to the hypereutrophic Stone Lake, De Pinto et al. (1976) required an alternative to a simple first-order decay rate to simulate the highly dynamic successional decline of phytoplankton functional group blooms. This apparent rapid response of heterotrophic activity to phytoplankton blooms was accounted for implicitly by including a second-order algal functional group decay term that was proportional to the product of the biomass of the group in question and the biomass of the entire phytoplankton assemblage.

In an attempt to account for the three governing factors already discussed for the degradation rate of phytoplankton biomass (phytoplankton physiological state, presence and character of the decomposer community, and seasonal response of decomposers), Rodgers and Salisbury (1981) proposed an alternative kinetic description of the process and applied it to Lake Michigan. The overall pseudo-first-order decomposition rate coefficient that they proposed included a temperature-dependent endogenous term plus a decomposer-mediated term that is a saturation function proportional to a trophic status indicator (chlorophyll concentration in this case) and inversely proportional to an indicator of phytoplankton physiological state (specific growth rate).

With respect to the significance of nonpredatory phosphorus recycle in lake primary productivity, even lakes receiving high external phosphorus loadings exhibit seasonal trends when the primary productivity appears to be controlled by recycled phosphorus. In performing a component analysis of phytoplankton–phosphorus dynamics in Saginaw Bay, Bierman et al. (1980) found that recycle from excretion and decomposition of phytoplankton contributed approximately 70% of the available phosphorus uptake during an August blue-green bloom. They also determined that microbial conversion of unavailable to available phosphorus contributed between 10 and 25% over the annual cycle to net phytoplankton phosphorus uptake. This significant result was determined even though Bierman used a relatively low first-order conversion rate coefficient of 0.005/d. (at 20°C), which is consistent with the regeneration rates observed in our study for the more tightly bound minimum cell quota phosphorus of the old *Scenedesmus* cultures.

Another example of the significance of the phosphorus recycle process can be found in Lake Erie. Lean et al. (1983) very effectively demonstrated extreme phytoplankton phosphorus limitation in the central basin of Lake Erie from June through August and in the eastern basin from August through September. Yet the central basin epilimnion data and model simulations of DiToro and Connolly (1980) exhibit the typical trend of peak phytoplankton growth rates and the beginning of a 3-mo nondiatom bloom in July. A similar trend is seen for the eastern basin epilimnion in late July and August. The component analysis of DiToro and Connolly (1980) and the sensitivity analysis of De Pinto et al. (1984) suggest that a major phosphorus source for these sustained late-summer blooms is phytoplankton release and microbial conversion from unavailable to available phosphorus.

Acknowledgments

We gratefully acknowledge the support provided to this investigation by the U.S. Environmental Protection Agency, ERL-Duluth, Large Lakes Research Station, Grosse Ile, MI, through grant No. R-804937 to Clarkson University. Partial travel support for presentation at the P–Plankton Dynamics Symposium and publication costs were provided by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI 48104.

References

BIERMAN, V. J. JR., AND D. M. DOLAN. 1981. Modeling of phytoplankton–nutrient dynamics in Saginaw Bay, Lake Huron. J. Great Lakes Res. 7:

409–439.

BIERMAN, V. J. JR., D. M. DOLAN, E. F. STOERMER, J. E. GANNON, AND V. E. SMITH. 1980. The development and calibration of a spatially simplified multi-class phytoplankton model for Saginaw Bay, Lake Huron. Great Lakes Environmental Planning Study (GLEPS). Contribution No. 33. Great Lakes Basin Commission.

BLOESCH, J., P. STADELMANN, AND H. BUHRER. 1977. Primary production, mineralization, and sedimentation in the euphotic zone of two Swiss lakes. Limnol. Oceanogr. 22: 511–522.

CHARLTON, M. N. 1975. Sedimentation: measurements in experimental enclosures. Verh. Int. Ver. Limnol. 19: 267–272.

DAFT, M. J., AND W. D. P. STEWART. 1973. Light and electron microscope observations on algal lysis by bacterium CP-1. New Phytol. 72: 799–806.

DE PINTO, J. V. 1982. An experimental apparatus for evaluating kinetics of available phosphorus release from aquatic particulates. Water Res. 16: 1065–1070.

DE PINTO, J. V., V. J. BIERMAN, JR., AND F. H. VERHOFF. 1976. Seasonal phytoplankton succession as a function of species competition for phosphorus and nitrogen, p. 141–170. *In* R. P. Canale [ed.] Modeling biochemical processes in aquatic ecosystems. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

DE PINTO, J. V., AND F. H. VERHOFF. 1977. Nutrient regeneration from aerobic decomposition of green algae. Environ. Sci. Technol. 11: 371–377.

DE PINTO, J. V., T. C. YOUNG, AND S. C. MARTIN. 1981. Algal-available phosphorus in suspended sediments from lower Great Lakes tributaries. J. Great Lakes Res. 7: 311–325.

DE PINTO, J. V., T. C. YOUNG, AND D. K. SALISBARY. 1984. A modeling analysis of the implications of phosphorus availability of Lake Erie inputs, p. 496–501. *In* M. Pirbazari and J. S. Devinny [ed.] Proceedings of 1984 Specialty Conference on Environmental Engineering. American Society of Civil Engineers, New York, NY.

DITORO, D. M., AND J. P. CONNOLLY. 1980. Mathematical models of water quality in large lakes, part 2: Lake Erie. US EPA Rep. No. 600/3-80-065.

DITORO, D. M., AND W. F. MATYSTIK, JR. 1979. Phosphorus recycle and chlorophyll in the Great Lakes. J. Great Lakes Res. 5: 233–245.

FALLON, R. D., AND T. D. BROCK. 1979. Decomposition of blue-green algal (cyanobacterial) blooms in Lake Mendota, Wisconsin. Appl. Environ. Microbiol. 37: 820–830.

GUILLARD, R. R. L., AND C. J. LORENZEN. 1972. Yellow-green algae with chlorophyllide C. J. Phycol. 8: 10–14.

GULLIVER, J. S., AND H. G. STEFAN. 1982. Lake phytoplankton model with destratification. J. Environ. Eng. Div., Proc. Am. Soc. Civ. Eng. 108: 864–882.

LARSON, D. P., H. T. MERCIER, AND K. W. MALUEG. 1973. Modeling algal growth dynamics in Shagawa Lake, Minnesota, p. 15–31. *In* E. J. Middlebrooks, D. H. Falkenborg, and T. E. Maloney [ed.] Modeling the eutrophication process. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

LEAN, D. R. S., A. P. ABBOTT, M. N. CHARLTON, AND S. S. RAO. 1983. Seasonal phosphate demand for Lake Erie plankton. J. Great Lakes Res. 9: 83–91.

MARTIN, S. C., J. V. DE PINTO, AND T. C. YOUNG. 1984. Biological availability of sediment phosphorus inputs to the lower Great Lakes. Final Report to ERL-Duluth, U.S. EPA for Grant No. CR807155. 170 p. (Available from NTIS)

MURPHY, J., AND J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27: 31–36.

REIM, R. L., AND M. S. SHANE. 1974. The characterization of a bacillus capable of blue-green bacteriocidal activity. Can. J. Microbiol. 20: 981–990.

RHEE, G. 1973. A continuous culture study of phosphate uptake, growth rate and polyphosphate in *Scenedesmus sp.* J. Phycol. 9: 495–506.

1980. Continuous culture in phytoplankton ecology, p. 151–203. *In* M. R. Droop and H. W. Jannasch [ed.] Advances in aquatic microbiology. Vol. 2. Academic Press, New York, NY.

RODGERS, P. W., AND J. V. DE PINTO. 1983. Estimation of phytoplankton decomposition rates using two-stage continuous flow studies. Water Res. 17: 761–769.

RODGERS, P. W., AND D. K. SALISBURY. 1981. Water quality modeling of Lake Michigan and consideration of the anomalous ice cover of 1976–1977. J. Great Lakes Res. 7: 467–480.

YOUNG, T. C., AND J. V. DE PINTO. 1982. Algal-availability of particulate phosphorus from diffuse and point source in the lower Great Lakes Basin, p. 111–119. *In* P. G. Sly [ed.] Sediment/freshwater interaction. Dr. W. Junk Publishers, The Hague, Netherlands.

YOUNG, T. C., J. V. DE PINTO, S. E. FLINT, M. S. SWITZENBAUM, AND J. K. EDZWALD. 1982. Algal availability of phosphorus in municipal wastewater. J. Water Pollut. Control Fed. 54: 1505–1516.

Dissolved Organic Phosphorus Compounds: Do They Satisfy Planktonic Phosphate Demand in Summer?[1]

Robert T. Heath

Department of Biological Sciences, Kent State University, Kent, OH 44242, USA

Heath, R. T. 1986. Dissolved organic phosphorus compounds: do they satisfy planktonic phosphate demand in summer? Can. J. Fish. Aquat. Sci. 43: 343–350.

The rate of release of phosphate from dissolved organic phosphorus (DOP) compounds generally accounted for <1% of the phosphate uptake rate by seston in the open water of five diverse freshwater systems in summer. Surface water samples were taken during July and August 1984 from a eutrophic lake (East Twin Lake, OH), an acid bog lake (Triangle Bog Lake, OH), a freshwater estuarine marsh that empties into the western basin of Lake Erie (Old Woman Creek, OH), and two large mainstem reservoirs on the Savannah River (R. B. Russel Reservoir and Clarks Hill Lake, GA). In each of these, phosphatase hydrolysable phosphomonoesters (PME) often were the major fraction of DOP; phosphate release from photosensitive DOP was not detected in any of these systems at this time. The rate of release of phosphate from PME was calculated from Michaelis–Menten kinetics, and phosphatase activity was estimated spectrophotometrically using *p*-nitrophenyl phosphate as a model substrate. Radiometric analysis of the rate of phosphate uptake by seston showed that phosphate was sorbed to seston by at least two different processes. The total uptake rate by all uptake processes exhibited an apparent first-order dependence on the concentration of available phosphate. Typically, the velocity of uptake was 1–10 $nmol \cdot L^{-1} \cdot min^{-1}$, and the velocity of release from PME was 0.01–0.06 $nmol \cdot L^{-1} \cdot min^{-1}$.

Le taux de libération de phosphate à partir de composés de phosphore organique dissous (POD) représentait en général moins de 1 % du taux d'absorption de phosphate par le seston présent dans l'eau libre de cinq différents bassins d'eau douce pendant l'été. On a prélevé des échantillons d'eau en surface en juillet et août 1984 dans un lac eutrophe (East Twin Lake, Ohio), dans un lac-tourbière acide (Triangle Bog Lake, Ohio), dans un marais estuarien d'eau douce qui se déverse dans le bassin ouest du lac Érié (Old Woman Creek, Ohio) et dans deux réservoirs importants situés dans l'embranchement principal du fleuve Savannah (R. B. Russel Reservoir et Clarks Hill Lake, Georgie). Dans chacun de ces endroits, des phosphates monoestérifiés (PME) hydrolysables par phosphatase constituaient souvent la majeure partie du POD; on n'a pas décelé pour l'instant de libération de phosphate à partir de POD photosensible dans aucun de ces systèmes. On a calculé le taux de libération de phosphate à partir des PME suivant la cinétique de Michaelis–Menten et l'activité de la phosphatase a été évaluée par spectrophotométrie en utilisant le phosphate de *p*-nitrophényle comme substrat type. L'analyse radiométrique du taux d'absorption de phosphate par le seston a révélé que cette absorption s'effectuait par au moins deux processus différents. Le taux total d'absorption par tous les processus a montré une dépendance apparente de premier ordre par rapport à la concentration de phosphate disponible. Typiquement, la vitesse d'absorption variait de 1 à 10 $nmol \cdot L^{-1} \cdot min^{-1}$ et la vitesse de libération à partir des PME de 0,01 à 0,06 $nmol \cdot L^{-1} \cdot min^{-1}$.

Received December 17, 1984
Accepted June 5, 1985
(J8045)

Reçu le 17 décembre 1984
Accepté le 5 juin 1985

Whether dissolved organic phosphorus (DOP) compounds are significant sources of phosphate for freshwater plankton is unknown. Hutchinson (1957) noted that DOP compounds often occurred in relative abundance at times of maximum phytoplankton productivity. From this he inferred that DOP may be an important autochthonous source of phosphate. Conversely it can be reasoned that these compounds are abundant because they are relatively refractory and are not significantly utilized as a phosphate source. Rigler (1968) and Berman (1970) observed that substantial portions of the "soluble unreactive phosphorus" (SUP) fraction of compounds appeared to be refractory to phosphate release. Francko and Heath (1979) demonstrated that the conditions essential for release of phosphate from DOP may not always be present in freshwater systems. Therefore, compounds may be refractory at one time but release phosphate at another. DOP compounds are significant sources of phosphate only if phosphate is released from them at a rate comparable with the planktonic assimilation rate of available phosphate. The purpose of this study was to determine whether the rate of release of phosphate from DOP satisfied planktonic phosphate demand in a variety of freshwater systems. Observations were confined to the summer when algal standing crops were maximal and available phosphate reached critically low concentrations.

[1]This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

Description of Lakes

The lakes studied were chosen because it was reasonable to expect them to have significant quantities of organic compounds. I reasoned that if DOP is a significant source of phosphate anywhere, it would be significant in lakes such as these.

East Twin Lake is a glacial kettle lake in a residential watershed about 7 km from Kent, Ohio. It has a surface area of 26.8 ha, a mean depth of 5.0 m, a maximum depth of 12.0 m, and a water residence time of 0.8 yr (Cooke et al. 1978). Before reclamation efforts in 1975 it was a typical "culturally eutrophic" lake supporting dense cyanobacterial populations each summer. Following application of aluminum sulfate, the transparency increased and phytoplankton populations were not dominated by cyanobacterial populations in the surface waters. The transparency was generally 1.5 m, the pH ranged from 7.5 to 8.5, and the alkalinity was about 2.2 meq $CaCO_3 \cdot L^{-1}$. Samples were drawn from the surface (0.1 m depth) over the deepest portion of the lake.

Triangle Bog Lake is an acidic dystrophic glacial lake in a relict bog managed by the Ohio Department of Natural Resources (ODNR). The lake has an area of 0.4 ha, a mean depth of 6.9 m, and a maximum depth of 8.1 m. It is bordered by a sphagnum shelf and is ringed by *Larix*. During late springtime, dense populations of the chloromonad *Gonyostomum semen* appear, but few algal cells are noted during the late summer. There are no apparent inlet streams; drainage by an outlet channel flows slowly if at all. The water is highly stained having a color of about 200 Pt units, a transparency of 0.45 m, pH 4.5–5.0, and alkalinity of 0.15 meq $CaCO_3 \cdot L^{-1}$. Further details of this bog lake were given by Buchanan (1982) and Cotner (1984). Samples were drawn from the surface over the deepest portion of the lake.

Old Woman Creek is a third-order stream that drains an agricultural watershed and widens into an open marsh that enters Lake Erie about 5 km east of Huron, Ohio. The marsh area has been designated a freshwater estuary and is managed as part of the National Estuarine Sanctuary program of the Department of the Interior through ODNR. The marsh has a mean depth of 0.5 m but the stream channel is approximately 2 m deep and 7 m wide. During the summer the mouth of the stream was blocked by sand dunes, preventing rapid flow of water from the marsh. The water in the stream channel generally had a transparency of 0.25 m and a pH of 8.1. Samples were taken from the surface in the stream channel approximately midway between the Darrow Road bridge (the upper boundary of the marsh) and the outlet into Lake Erie.

Clarks Hill Lake and R. B. Russel Reservoir are large mainstem reservoirs on the Savannah River bounding Georgia and South Carolina. Clarks Hill Lake was established in 1952. It has a surface area of 29 000 ha and a length of 63 km. During the summer the transparency was 2.0 m, pH was 7.3, and alkalinity was 0.3 meq $CaCO_3 \cdot L^{-1}$. Water for this study was taken from the surface at a site about 3 km downstream from the plunge point. It was nutrient-poor water having a relatively large standing crop of phytoplankton. R. B. Russel Reservoir was filled during the spring of 1984 following completion of the R. B. Russel Dam at the upper boundary of Clarks Hill Lake. It extends the full 42-km distance from Lake Hartwell reservoir to Clarks Hill Lake reservoir. It has a surface area of 10 800 ha. The transparency in the summer was 2.0 m, pH was 7.1, and alkalinity was 0.2 meq $CaCO_3 \cdot L^{-1}$. Water for this study was taken from a station within 1 km of Russel Dam.

Methods

All glassware and bottles were acid rinsed and autoclaved before use. Millipore HA filters were prepared by passing three rinses of 5 mL of 1 mol $HCl \cdot L^{-1}$ followed by three rinses of filtered, distilled, autoclaved water.

Water samples were collected in polyethylene bottles. Portions were filtered through Millipore HA (0.45 μm) filters at 0.5 Pa. Water samples collected from R. B. Russel Reservoir and Clarks Hill Lake were filtered on site, and portions of both filtered and unfiltered water samples were shipped to Kent State University and received within 24 h of collection. All other water samples were returned to the university within 4 h of collection.

All tests for detection of phosphorus content were performed in triplicate. Soluble reactive phosphorus (SRP) was determined by the colorimetric molybdenum blue, ascorbic acid method of Murphy and Riley (1962) as modified by the U.S. Environmental Protection Agency (USEPA 1971). Total phosphorus content of unfiltered water (TP) and filtered water (TSP) were determined following hydrolysis with persulfate at 2 Pa and 124°C for 60 min (USEPA 1971).

Photosensitive phosphorus compounds were detected as the increase in SRP following irradiation with a low-intensity ultraviolet lamp, as previously described by Francko and Heath (1979). Phosphomonoesters were detected as the increase in SRP following incubation with calf intestinal mucosa alkaline phosphatase (0.05 $mg \cdot L^{-1}$, Sigma) in 0.01 mol *tris*-hydroxymethyl aminomethane $\cdot L^{-1}$ and 0.001 mol $MgCl_2 \cdot L^{-1}$ at pH 9.0 and 37°C for 24 h (Heath and Cooke 1975; Boavida and Heath 1984). Concentration was determined by comparison with a standard dilution series of glucose-6-phosphate (Sigma).

Alkaline phosphatase activity was detected spectrophotometrically using *p*-nitrophenyl phosphate (pNPP) as a model substrate. Unfiltered lake water samples were incubated with 1×10^{-3} mol pNPP $\cdot L^{-1}$ at ambient conditions in 1×10^{-3} mol *tris*-hydroxymethyl aminomethane $\cdot L^{-1}$, pH 9.0. Acid phosphatase activity was detected using 1×10^{-3} mol pNPP $\cdot L^{-1}$ and 1×10^{-3} mol acetate buffer $\cdot L^{-1}$, pH 5.0. Velocity of substrate hydrolysis was determined as the rate of *p*-nitrophenol production, detected as increase in absorbance at 395 nm at pH 9.0 in 1-cm quartz cuvettes. Alkaline phosphatase tests were read at 30-min or 1-h intervals. Acid phosphatase tests were run in several replicates. At hourly intervals a replicate acid phosphatase test was removed, the pH adjusted to 9.0, the absorbance determined, and then discarded. The change in absorbance was expressed as nanomoles *p*-nitrophenol released per litre by comparison with a standard solution of *p*-nitrophenol in 1×10^{-3} mol *tris* hydroxymethyl aminomethane $\cdot L^{-1}$, pH 9.0.

The K_m and V_{max} were determined by the method of Hanes (1932). Substrate concentrations of 5×10^{-5} to 8×10^{-4} mol $\cdot L^{-1}$ were used. The substrate concentration divided by the inverse of the initial rate of hydrolysis was regressed against the substrate concentration; r^2 generally was greater than 0.96.

The rate of phosphate sorbtion to seston was determined radiometrically by collecting particles on Millipore HA filters that were pretreated and postrinsed to remove nonparticulate radiolabelled phosphate. Millipore HA filters were presoaked in 0.5 nmol $KH_2PO_4 \cdot L^{-1}$. Unfiltered 50-mL portions of lake water were incubated in a water bath adjusted to ambient lake temperature. At time zero, about 4×10^4 Bq carrier-free acid-free ^{32}P-orthophosphate (New England Nuclear) was added to

TABLE 1. Phosphorus composition of lake water and the rate of enzymatic release of phosphate from phosphomonoesters (PME). The rate of release of phosphate from PME (v_{rel}) was calculated as nanomolar flux (nmol·L^{-1}·min^{-1}) using Michaelis–Menten kinetics. Phosphatase activity (V_{max}) and the K_m were determined using *p*-nitrophenyl phosphate as a model substrate. The K_m was not routinely determined; when not determined, the value used for calculation is shown in parentheses.

	Total P (μg·L^{-1})	SUP (μg·L^{-1})	PME		V_{max} (nmol·L^{-1}·min^{-1})	K_m (mmol·L^{-1})	v_{rel} (nmol·L^{-1}·min^{-1})
			μg·L^{-1}	nmol·L^{-1}			
Old Woman Creek							
17 July	331.1	21.2	16.2	552.6	87.32	0.40	0.120
31 July	362.2	36.0	10.5	338.7	22.20	(0.40)	0.019
6 Sept.	259.1	14.9	2.7	87.1	24.44	0.32	0.007
Clarks Hill Lake							
19 July	30.6	16.2	0.0	0.0	43.10	0.25	0.000
8 Aug.	65.9	15.4	10.3	332.3	18.29	(0.25)	0.024
Triangle Bog Lake							
7 Aug.	37.8	8.5	6.9	221.9	327.8	0.35	0.208
25 Sept.	30.8	6.2	2.6	85.6	245.4	0.36	0.058
East Twin Lake							
26 July	31.8	27.8	23.9	771.1	28.1	0.42	0.052
16 Aug.	22.9	7.8	5.7	183.9	43.7	(0.42)	0.019
R. B. Russel Reservoir							
19 July	17.6	11.1	2.9	95.0	37.13	0.15	0.023
8 Aug.	13.6	14.9	15.4	496.8	32.84	(0.15)	0.108

the swirled sample. Aliquots of 1 mL were removed with an automatic pipet affixed with a sterile polyethylene tip at timed intervals of 30, 100, 200, 300, 400, 500, and 1000 s after addition of radiolabel. The aliquots of 1 mL were filtered through phosphate-soaked Millipore HA filters at a pressure of 0.5 Pa; the filters were then rinsed with three 10-mL portions of distilled water. The filters were air-dried, placed into Beckman Biogamma vials containing 2.5 mL of Scintillene (Fisher Scientific) liquid scintillation cocktail, and counted in a Beckman 6800 liquid scintillation spectrometer. The detected count rate was automatically corrected for quench, so differences in quenching from one sample to another were not a factor in the reported count rate of particulate material adhering to the filter (X). Total radioactivity per millilitre (P_0) was determined by placing 1.0 mL of the radioactive lake water into 7 mL of Beckman RediSolv MP water-accepting liquid scintillation cocktail. Values of $\ln [P_0/(P_0 - X)]$ were regressed against t, the time of filtration. This yielded a straight line from the origin with positive slope, K. Points were added sequentially to the regression until r^2 dropped below 0.99, identifying a break in the curve.

Results

Release of Phosphate from DOP

Francko and Heath (1979) reported the release of phosphate from two different classes of dissolved organic compounds. One of these classes had a high molecular weight and released phosphate following irradiation with sunlight in an event coincident with the photoreduction of ferric ions associated with these compounds (Francko and Heath 1982, 1983). These compounds co-chromatographed with humic acids both in Sephadex and in anion-exchange chromatography. The rate of phosphate release from these humic compounds appeared to be limited by a process involving the availability of bound ferric ion to an electron donor within the compound. Phosphate is released from another class of low molecular weight compounds, phosphomonoesters (PME), through the hydrolytic action of phosphatases. The rate of release of phosphate from these phosphatase-sensitive compounds depends on the enzyme activity present in the lake water and the parameters controlling the kinetics of those enzymes. Phosphatases generally are not homotropically modulated by their substrates and show simple kinetics (Fernley 1971). The velocity of release of phosphate from PME can be calculated from the Michaelis–Menten equation following determination of the substrate concentrations, the collective maximal velocity (V'_{max}), and the collective Michaelis constant (K'_m) of the enzymes present in the water. The enzyme variables V'_{max} and K'_m of the collective activity in the lake were determined using pNPP as a model substrate.

Although the freshwater systems differed widely in total phosphorus content of the open water, the content of the SUP components only ranged from 6 to 39 μg·L^{-1} (Table 1). At no time during this study was any photosensitive phosphate release detected in any of these lakes. PME comprised a variable portion of the SUP, ranging from none to 100%. Usually, PME comprised between 25 and 70% of the SUP. The PME content tended to decrease over time in each of these lakes. Enzyme activity, expressed as V'_{max}, ranged from being moderately active acid phosphatase in Triangle Bog Lake to barely detectable alkaline phosphatase activity in the Old Woman Creek open marsh. Phosphatase activity did not appear to change greatly through the season in any of the systems examined. Although the K'_m was not routinely determined in this study, I assumed that it would be similar to those values most recently determined in each system. When the K'_m was not determined, the value used for calculation of velocity is shown within parentheses in Table 1. The rate of release of phosphate from PME was estimated in terms of nanomolar flux (nanomoles per litre per minute).

Phosphate Uptake by Seston

Uptake rates can be calculated if the kinetic dependence on phosphate can be determined and the phosphate concentration present in the water is known. Kinetics of phosphate uptake

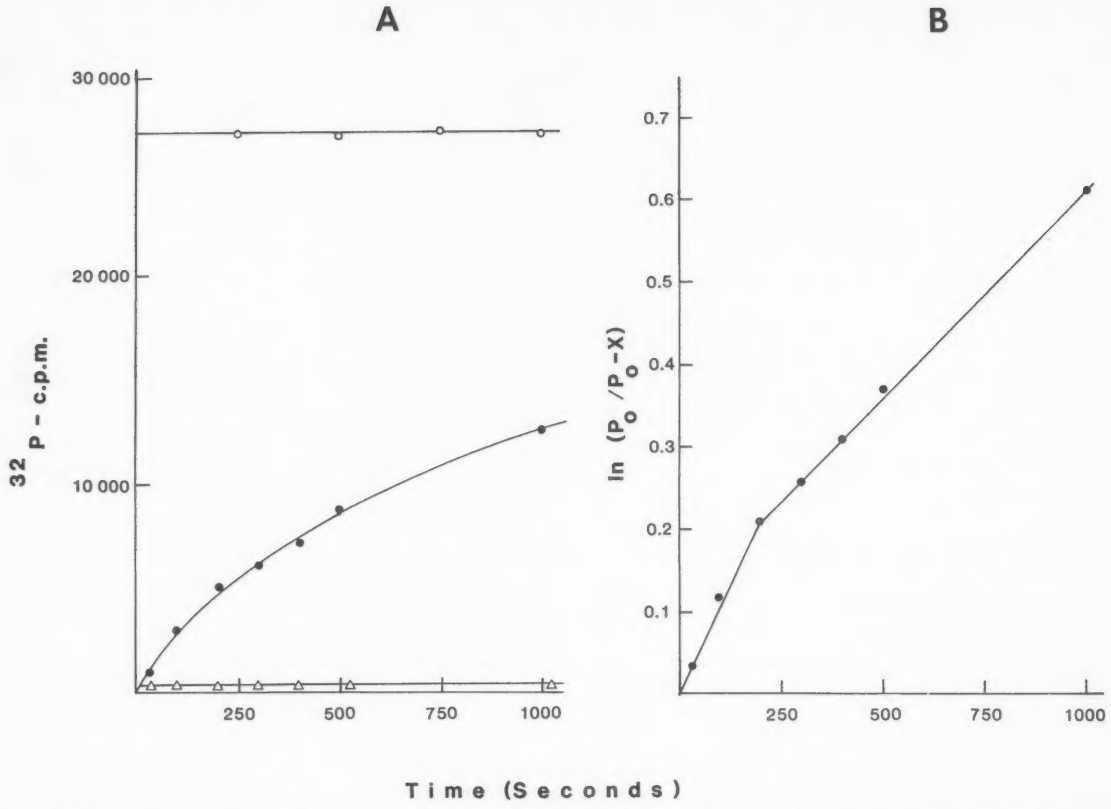


FIG. 1. Carrier-free ^{32}P-orthophosphate was added to 50 mL of unfiltered water collected from the surface of Old Woman Creek on 6 September 1984 to give a final activity of 4.52×10^2 Bq·mL^{-1}. Also, radiolabelled phosphate was added to a 50-mL portion that had been prefiltered through a Millipore HA filter to give a final activity of 4.27×10^2 Bq·mL^{-1}. Both filtered and unfiltered samples were incubated in a water bath maintained at 17°C, the water temperature at time of collection. (A) Total activity in 1-mL aliquots, cpm vs. time (○), activity in 1-mL aliquots of unfiltered lake water retained on Millipore HA filters presoaked in 0.5 mol $KH_2PO_4 \cdot L^{-1}$ (●), and activity in 1-mL aliquots of prefiltered water retained on presoaked Millipore HA filters (△); (B) Proportion of total activity in 1-mL aliquots of unfiltered water retained on presoaked Millipore HA filters expressed as ln $(P_0/P_0 - X)$ vs. time.

were determined by adding tracer quantities of radiolabelled orthophosphate to lake water samples that were assumed to be in a dynamic equilibrium. Uptake by seston was followed directly by collecting timed aliquots on separate filters and then washing and drying each filter and counting the radioactivity retained on the filter. Millipore HA filters retained more labelled material than Whatmann GF/A (3.0 μm), Whatman GF/F (1.2 μm), and Nucleopore (0.6 μm) filters. Also, Millipore GS (0.22 μm), Gelman Metricel GA-8 (0.20 μm), and Nucleopore (0.2 μm) filters retained no more label than did Millipore HA; in fact, Nucleopore (0.2 μm) often retained less. A drawback of this method is that phosphate and other dissolved compounds may artifactually bind to the filter and thereby elevate the estimate of the proportional uptake rate constants. Addition of radiotracer to lake water that was prefiltered through Millipore HA filters showed that artifactual binding of nonparticulate radioisotope was virtually eliminated by presoaking the filters in 0.5 mol $KH_2PO_4 \cdot L^{-1}$. Only 1.5 ± 0.3 Bq was retained on presoaked filters through which was passed 4.5×10^2 Bq in 1.0 mL of prefiltered lake water. The total amount of radiotracer detected remained unchanged over the duration of the test, indicating that none was lost to the sides of the flask, altering its availability to suspended particles (Fig. 1A). For these reasons I believe that the radioactive material retained on the filters was an accurate indication of ^{32}P-phosphate that had moved from solution to suspended particles.

If uptake exhibits a first-order dependence on phosphate remaining available in solution, the uptake velocity (V) is

$$(1) \quad V = \frac{dX}{dt} = K(P)$$

where X is the amount taken up by particles at time t, P is the amount of dissolved phosphate available at that time, and K is the proportion of P taken up per unit time. Because P is that portion of the initial amount of phosphate (P_0) not yet taken up by particles, equation (1) can be expressed as

$$(2) \quad \frac{dX}{dt} = K(P_0 - X).$$

Its integrated form is

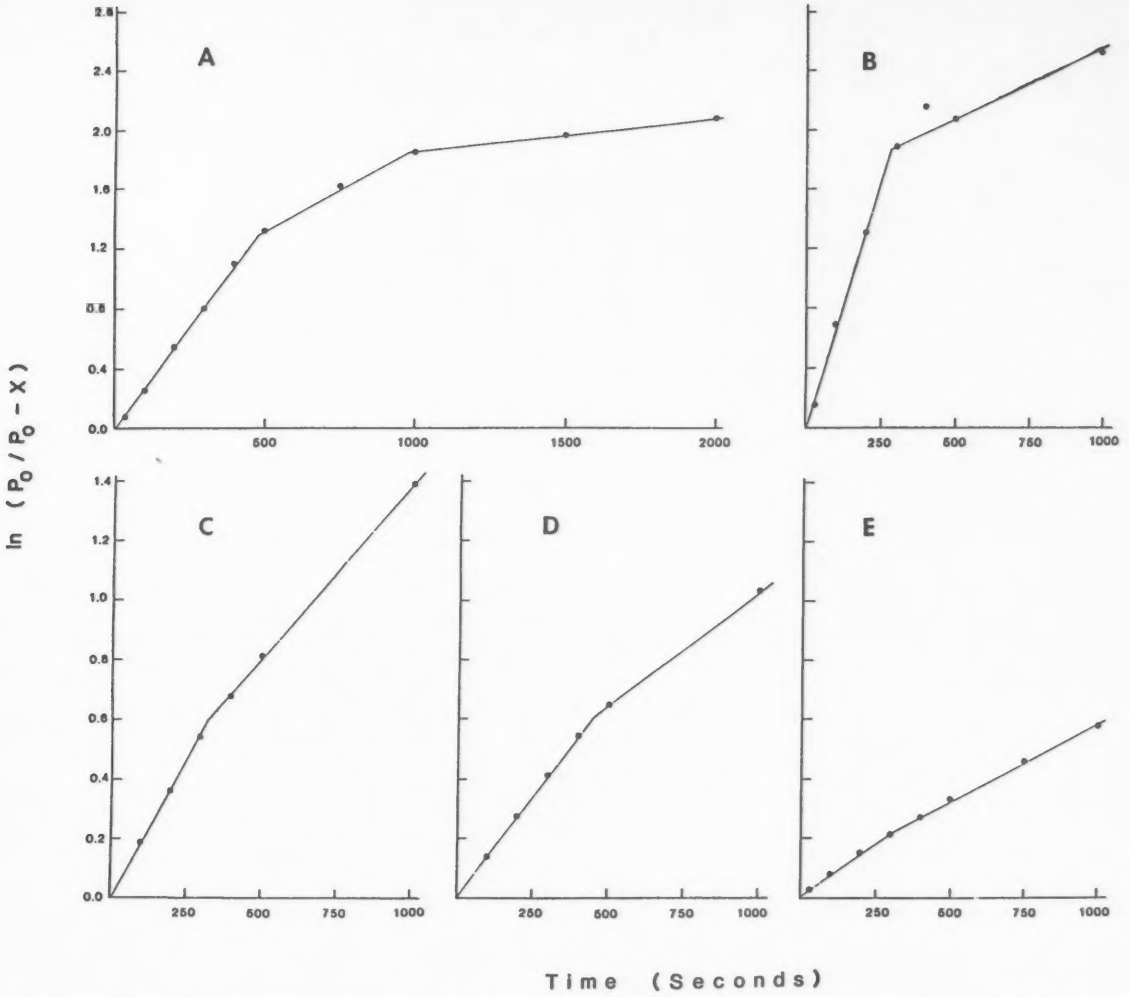


FIG. 2. Proportional phosphate uptake expressed as ln $(P_0/P_0 - X)$ vs. time. (A) East Twin Lake, 16 August 1984, 25°C; (B) Triangle Bog Lake, 15 August 1984, 25°C; (C) R. B. Russel Reservoir, 19 July 1984, 30°C; (D) Clarks Hill Lake, 9 August 1984, 27°C; (E) Old Woman Creek, 31 July 1984, 23°C.

$$(3)\quad \ln\left(\frac{P_0}{P_0 - X}\right) = Kt.$$

Plotting values of $\ln [P_0/(P_0 - X)]$ against t gives a straight line that passes through the origin only if this uptake is first-order dependent on phosphate concentration (Latham 1964).

The overall first-order dependence on available phosphate is apparent from the straight line passing through the origin (Fig. 1B, Fig. 2). This initial slope was determined by linear regression of those values observed in the first several hundred seconds of the test. The regression coefficient was consistently high (generally r^2 was greater than 0.99). Replicate determinations yielded lines with similar initial slopes generally within a standard deviation of 3% of the mean slope. This initial slope, the overall rate constant K, is the proportion of available phosphate removed per unit time by all processes. Often the slope of this line showed an abrupt change after several hundred seconds, yielding a second line with a lower slope, indicating that uptake was not accomplished by a single first-order process.

These observations, similar to those of Lean (1976), are consistent with the view that at least two processes or classes of processes were involved in uptake. One process was relatively rapid and the compartment into which phosphate was taken became saturated and reached a steady state generally within 500 s after initiation of the test. Net uptake by the slower process continued for 30 min to several hours until only a few percent of P_0 remained in solution. Because this study was conducted to characterize rate of phosphate removed to seston by all processes, only the initial slope, K, was used for calculation of the velocity of uptake in equation (1). Phosphate was estimated as SRP by a standard molybdenum blue colorimetric procedure.

The wide variety of phosphate turnover times, shown in

TABLE 2. Phosphate uptake rate and comparison with the rate of release of phosphate from PME. The turnover time (T) and its inverse, the overall uptake rate constant, k, were determined radiometrically. The velocity of phosphate uptake (v_{up}) was compared with the velocity of phosphate release from PME (v_{rel}) in nanomolar flux units and expressed as a fraction of v_{up} satisfied by v_{rel}.

	T (min)	K (min^{-1})	SRP		v_{up} ($nmol \cdot L^{-1} \cdot min^{-1}$)	v_{rel} ($nmol \cdot L^{-1} \cdot min^{-1}$)	v_{rel}/v_{up}
			$\mu g \cdot L^{-1}$	$nmol \cdot L^{-1}$			
Old Woman Creek							
17 July	173.1	0.0058	11.2	361.3	2.09	0.120	0.0574
31 July	127.4	0.0078	12.8	412.9	3.24	0.019	0.0059
6 Sept.	26.3	0.0381	1.7	55.5	2.11	0.007	0.0033
Clarks Hill Lake							
19 July	11.8	0.0844	3.1	101.3	8.55	0.000	0.0000
8 Aug.	12.9	0.0773	1.9	60.6	4.68	0.024	0.0051
Triangle Bog Lake							
7 Aug.	1.0	0.9756	2.8	90.3	88.12	0.208	0.0024
25 Sept.	2.4	0.4226	14.3	461.3	194.94	0.058	0.0003
East Twin Lake							
26 July	9.0	0.1116	5.3	170.0	18.97	0.052	0.0027
16 Aug.	6.2	0.1610	1.8	59.3	9.55	0.019	0.0020
R. B. Russel Reservoir							
19 July	10.7	0.0932	3.7	119.0	11.09	0.023	0.0021
8 Aug.	12.5	0.0799	0.6	18.1	1.45	0.108	0.0745

Table 2, indicates that these systems differed greatly in their phosphate demand. Lean et al. (1983) reported that phosphate turnover times greater than 30 min indicated that phytoplankton likely were not limited by P availability. Old Woman Creek seston very slowly removed available phosphate from the water, suggesting that P was not a limiting factor in that system. By contrast, seston in Triangle Bog Lake turned over phosphate at a rate suggestive of extreme P limitation. Despite these wide differences in turnover time, the velocity of uptake was surprisingly similar in the various systems studied. In general, the velocity of uptake ranged between 1 and 10 $nmol \cdot L^{-1} \cdot min^{-1}$. Only Triangle Bog Lake differed greatly from the others in overall uptake rate. I speculate that this difference may result from dominance by bacterioplankton rather than phytoplankton in that lake. In a laboratory chemostat study, Rhee (1972) demonstrated with a mixed culture of *Scenedesmus* and *Pseudomonas* that the bacteria successfully competed for phosphate, ostensibly because of more rapid growth and greater phosphate uptake rate.

Comparison of the rate of release and the rate of phosphate uptake on each day (Table 2) showed that in none of the systems studied was phosphate released from PME at a rate sufficient to satisfy the apparent phosphate demand. I conclude that DOP compounds did not represent nutritionally important sources of phosphate to the summer planktonic communities in the variety of freshwater systems studied.

Discussion

In nearly all cases examined, DOP apparently released phosphate at a rate insufficient to satisfy even 1% of planktonic phosphate demand. This conclusion is based on a comparison of an indirect measurement (phosphate release from PME calculated from observations of K_m, V_{max}, and PME concentration) with a measurement of phosphate uptake using SRP to estimate available phosphate. Although quantitative errors could arise in either of these measurements, it is unlikely that errors would be sufficient to alter the overall conclusion. If this conclusion is erroneous, it results from an error of greater than two orders of magnitude. An overestimate of K_m or an underestimate of V_{max} by this magnitude seems unlikely.

I assumed that the use of pNPP as a model substrate provided a reasonable estimate of phosphatase activity. Bacterial alkaline phosphatase (Reid and Wilson 1971) and mammalian alkaline phosphatases (Fernley 1971) appear to accept pNPP and natural substates equally well (i.e. the K_m values for pNPP and natural substrates are similar); acid phosphatases often hydrolyze pNPP somewhat faster than natural substrates (Hollander 1971). This artificial substrate has been shown in some cases to be a reliable model substrate for the investigation of some algal phosphatases (Flint and Hopton 1977), although this has not yet been demonstrated in a wide variety of eukaryotic algae likely to occur in lakes such as those studied (Cembella et al. 1983). Also, natural substrates would likely act as competitive inhibitors of this model reaction, decreasing the rate of hydrolysis of pNPP. Competitive inhibitors increase the apparent K_m for pNPP by a factor of $(1 + I/K_i)$ (Cornish-Bowden 1979), where I is the concentration of natural substrates and K_i is the Michaelis constant of the enzyme for these natural substrates that I assumed was to equal the K_m for pNPP. The presence of natural substrates probably caused no greater than a 10% error in the estimate of the K_m for pNPP, because PME concentration was usually less than 1×10^{-6} $mol \cdot L^{-1}$.

The concentrations of naturally occurring substrates were determined as the increase in detectable SRP in filtered lake water after incubation with calf intestinal mucosa alkaline phosphatase. This enzyme hydrolyzes a broad variety of PME as well as certain polyphosphates (Fernley and Walker 1967). Because not all phosphatases accept as broad a range of substrates as this enzyme, this estimate of the concentration of phosphatase-sensitive compounds likely is an upper limit of the substrate concentration available to naturally occurring enzymes.

These results compare favorably with those previously reported. East Twin Lake, before reclamation efforts were completed, was a eutrophic lake with a transparency of less than 0.2 m at the height of the summer bloom of *Aphanizomenon flos-aquae* during the summer seasons of 1972 and 1973 (Heath

and Cooke 1975). In each year the phosphatase activity increased greatly toward the end of the growing season. The K_m of natural enzymes for pNPP was 3.2×10^{-4} mol·L^{-1} and V_{max} ranged from 18 to 398 nmol·L^{-1}·min^{-1}. The calculated velocity of release ranged from 0.009 to 0.121 nmol·L^{-1}·min^{-1}, a range of velocities similar to those observed in this study. Also, Berman (1970) reported that the K_m for pNPP ranged from 1.3×10^{-5} to 6.7×10^{-4} mol·L^{-1} and that V_{max} ranged from 3.3 to 21.0 nmol·L^{-1}·min^{-1}.

Errors in the measurement of the phosphate uptake rate probably did not arise in the estimate of the proportional uptake rate, K, and its inverse, T, the turnover time. The turnover times noted in this study are within the range of previously reported values. Rigler (1964) observed turnover times as short as several minutes. Lean et al. (1983) observed phosphate turnover times longer than 1 h on Lake Erie, and Perry and Eppley (1981) reported phosphate turnover times of 200 d in the surface waters of the California Current.

A more likely source of error in the reported phosphate uptake was the use of SRP to estimate available phosphate concentration. Using primarily a bioassay procedure, Rigler (1966, 1968) elegantly argued that SRP may often greatly overestimate available phosphate, perhaps by two orders of magnitude. He reported that the bioassay generally estimated available phosphate to be between 4 and 8% of SRP. Therefore, even if the Rigler bioassay were used to estimate phosphate concentration, it seems unlikely that it would consistently account for differences of the magnitude sufficient to alter the conclusion of this study. Chamberlain and Shapiro (1969) compared a bioassay with the phosphate detectable after extraction of its molybdyl-derivative into isobutanol. They showed that in many lakes the SRP and the phosphate detected after extraction were similar and corresponded to that available to P-starved cultures of *Microcystis aeruginosa*. Recently, Nürnberg and Peters (1984) have shown that SRP often is a reliable estimate of available phosphate in a variety of lakes. Also, Francko and Heath (1979) showed that greater than 90% of SRP chromatographed as phosphate in anion exchange and gel permeation chromatography. For these reasons I used this method to estimate phosphate concentrations throughout this study on these lakes, and the velocity of phosphate uptake was calculated as the K proportion of SRP.

Our results indicate the DOP compounds are not major sources of phosphate at the height of the growing season, but little is known of the distribution and occurrence of such compounds throughout the year. Previously we have observed that PME were in greatest abundance in the late springtime in East Twin Lake (Heath and Cooke 1975). Recently, Cotner (1984) has observed in Triangle Bog Lake that both PME and photosensitive humic compounds were in abundance early in the springtime and decreased to a minimum during the growing season. Such studies suggest that DOP compounds may be most important in the early development of the planktonic community in the spring rather than in the late summer.

Even if DOP compounds are significant P sources in some seasons other than summer, why does phosphatase appear in such abundance during summer phytoplankton blooms? This study suggests that phosphatases are without substantial nutritional benefit. Many have noted that phosphatase specific activity (i.e. activity per unit biomass) increased following P limitation and depletion of internal stores of P (Fitzgerald and Nelson 1966; Berman 1970; Pettersson 1980). We noted that an increase in enzyme specific activity was related to an increase in potential productivity and growth of a population of *Aphanizomenon flos-aquae* in East Twin Lake (Heath and Cooke 1975). That relationship was consistent with the view that enzyme synthesis, induced by P limitation, resulted in release of sufficient phosphate from DOP to satisfy the phosphate demand and to support substantial growth of the cyanobacterial population. That is, our earlier work related phosphatase with significant activity of a phytoplankton population; current work now suggests that there was negligible nutritional benefit derived from what DOP may have been hydrolyzed by these enzymes.

These findings taken together suggest that DOP compounds may be important to plankton but in non-nutritive ways. Recent studies in freshwater lakes have detected the presence of physiologically significant quantities of DOP compounds known to control and regulate cell function (Amblard 1981). Francko and Wetzel (1982) and Francko (1983) detected nanomolar quantities of cyclic adenosine 3′,5′-monophosphate (cAMP) in a wide variety of freshwater lakes. They observed that cAMP concentrations were related to primary productivity. Laboratory studies have shown that such quantities are able to regulate metabolic activities of algal cells in culture (Handa et al. 1981; Francko and Wetzel 1981). Notably, cAMP and related compounds may control alkaline phosphatase activity in phytoplankton (Francko 1985). DOP compounds may be informational messengers controlling plankton metabolism. The hydrolytic enzymes in turn may attenuate that signal. I believe that future studies of DOP compounds should take this broader view and consider the possibility that these compounds and their associated enzymes are involved in the control and regulation of the metabolic activities of the planktonic community.

Acknowledgments

I thank Susan MacMillan and William Lamberts for their technical assistance. This study was supported in part by a grant from the National Oceanic and Atmospheric Administration, Office of Ocean and Coastal Resource Management, that was administered through the Ohio Department of Natural Resources ODNR-ENC 990973, by an Intergovernmental Personnel Agreement from the U.S. Department of the Army, Corps of Engineers, and by the Kent State University, Department of Biological Sciences. Partial travel support and publication costs were provided by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI 48104.

References

AMBLARD, C. 1981. Intérêts du dosage des adenosine 5-phosphate pour l'étude de la dynamique des populations phytoplanktoniques lacustres. Hydrobiologia 85: 257–270.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

BOAVIDA, M. J., AND R. T. HEATH. 1984. Are the phosphatases released by *Daphnia magna* components of its food? Limnol. Oceanogr. 29: 641–645.

BUCHANAN, E. L. 1982. Planktonic photoheterotrophic and heterotrophic uptake of glucose in two acid lakes and one eutrophic lake in northeastern Ohio. Ph.D. dissertation, Kent State University, Kent, OH. 177 p.

CEMBELLA, A. D., N. J. ANTIA, AND P. J. HARRISON. 1983. The utilization of inorganic and organic phosphorus compounds as nutrients by eukaryotic microalgae: a multidisciplinary perspective. CRC Crit. Rev. Microbiol. 10(4): 317–391.

CHAMBERLAIN, W. M., AND J. SHAPIRO 1969. On the biological significance of phosphate analysis; comparison of standard and new methods with a bioassay. Limnol. Oceanogr. 14: 921–927.

COOKE, G. D., R. T. HEATH, R. H. KENNEDY, AND M. R. MCCOMAS. 1978. Effects of diversion and alum application on two eutrophic lakes. U.S.

EPA Ecological Research Series EPA-600/3-78-033.

CORNISH-BOWDEN, A. 1979. Fundamentals of enzyme kinetics. Butterworths, London. 230 p.

COTNER, J. B. 1984. Significance of dissolved phosphorus compounds in an acid bog lake. M.S. thesis, Kent State University, Kent, OH. 116 p.

FERNLEY, H. N. 1971. Mammalian alkaline phosphatases, p. 417–447. *In* P. D. Boyer [ed.] The enzymes. Vol. 4. Academic Press, New York, NY.

FERNLEY, H. N., AND P. G. WALKER. 1967. Studies on alkaline phosphatase. Inhibition by phosphate derivatives and the substrate specificity. Biochem. J. 104: 1011–1018.

FITZGERALD, G. T., AND T. D. NELSON. 1966. Extractive and enzymatic analyses for limiting or surplus phosphorus in algae. J. Phycol. 2: 32–37.

FLINT, K. P., AND J. W. HOPTON. 1977. Substrate specificity and ion inhibition of bacterial and particle associated alkaline phosphatases of waters and sewage sludges. Eur. J. Appl. Microbiol. 4: 195–204.

FRANCKO, D. A. 1983. Dissolved cyclic adenosine 3′:5′ monophosphate (cAMP) in a eutrophic reservoir lake. Proc. Okla. Acad. Sci. 63: 9–11.

FRANCKO, D. A. 1985. Phytoplankton metabolism and cyclic nucleotides. II. Nucleotide-induced perturbations of alkaline phosphatase activity. Arch. Hydrobiol. 100: 409–421.

FRANCKO, D. A., AND R. T. HEATH. 1979. Functionally distinct classes of complex phosphorus compounds in lake water. Limnol. Oceanogr. 24: 463–473.

1982. UV-sensitive complex phosphorus: association with dissolved humic material and iron in a bog lake. Limnol. Oceanogr. 27: 564–569.

1983. Abiotic uptake and photodependent release of phosphate from high-molecular-weight humic–iron complexes in bog lakes, p. 467–480. *In* R. F. Christman and E. T. Gjessing [ed.] Aquatic and terrestrial humic material. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

FRANCKO, D. A., AND R. G. WETZEL. 1981. Dynamics of cellular and extracellular cAMP in *Anabaena flos-aquae* (Cyanophyta): intrinsic culture variability and correlation with metabolic variables. J. Phycol. 17: 129–134.

1982. The isolation of cyclic adenosine 3′:5′-monophosphate (cAMP) from lakes of differing trophic status: correlation with planktonic metabolic variables. Limnol. Oceanogr. 27: 27–38.

HANDA, A. K., R. A. BRESSAN, H. QUADER, AND P. FILNER. 1981. Association of formation and release of cyclic AMP with glucose depletion and onset of chlorophyll synthesis in *Poteriochromonas malhamensis*. Plant Physiol. 68: 460–463.

HANES, C. S. 1932. The effect of starch concentration upon the velocity of hydrolysis by the amylase of germinated baley. Biochem. J. 26: 1406–1421.

HEATH, R. T., AND G. D. COOKE. 1975. The significance of alkaline phosphatase in a eutrophic lake. Verh. Int. Ver. Limnol. 19: 959–965.

HOLLANDER, V. P. 1971. Acid phosphatases, p. 449–498. *In* P. D. Boyer [ed.] The enzymes. Vol. 4. Academic Press, New York, NY.

HUTCHINSON, G. E. 1957. A treatise on limnology. Vol. 1, part 2. Wiley, New York, NY. 1015 p.

LATHAM, J. L. 1964. Elementary reaction kinetics. Butterworths, London. 175 p.

LEAN, D. R. S. 1976. Phosphorus kinetics in lake water: influence of membrane filter pore size and low-pressure filtration. J. Fish. Res. Board Can. 33: 2800–2804.

LEAN, D. R. S., A. P. ABBOTT, M. N. CHARLTON, AND S. S. RAO. 1983. Seasonal phosphate demand for Lake Erie plankton. J. Great Lakes Res. 9: 83–91.

MURPHY, J., J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27: 31–36.

NÜRNBERG, G., AND R. H. PETERS. 1984. Biological availability of soluble reactive phosphorus in anoxic and oxic freshwaters. Can. J. Fish. Aquat. Sci. 41: 757–765.

PERRY, M. J., AND R. W. EPPLEY. 1981. Phosphate uptake by phytoplankton in the central north Pacific Ocean. Deep-Sea Res. 28A: 39–49.

PETTERSSON, K. 1980. Alkaline phosphatase activity and algal surplus phosphorus as phosphorus-deficiency indicators in Lake Erken. Arch. Hydrobiol. 89: 54–87.

REID, T. W., AND I. B. WILSON. 1971. *E. coli* alkaline phosphatase. p. 473–415. *In* P. D. Boyer [ed.] The enzymes. Vol. 4. Academic Press, New York, NY.

RHEE, G. Y. 1972. Competition between an alga and an aquatic bacterium for phosphate. Limnol. Oceanogr. 17: 505–514.

RIGLER, F. H. 1964. The phosphorus fractions and the turnover time of inorganic phosphorus in different types of lakes. Limnol. Oceanogr. 9: 511–518.

1966. Radiobiological analysis of inogranic phosphorus in lake water. Verh. Int. Ver. Limnol. 16: 465–470.

1968. Further observations inconsistent with the hypothesis that molybdenum blue method measures orthophosphate in lake water. Limnol. Oceanogr. 13: 7–13.

USEPA 1971. Methods for chemical analysis of water and wastes. Natl. Environ. Res. Ctr., Cincinnati, OH.

Dynamics of Lake Michigan Natural Phytoplankton Communities in Continuous Cultures Along a Si:P Loading Gradient[1]

Susan Soltau Kilham

Division of Biological Sciences, The University of Michigan, Ann Arbor, MI 48109-1048, USA

Kilham, S. S. 1986. Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient. Can. J. Fish. Aquat. Sci. 43: 351–360.

The hypothesis that phytoplankton species assort themselves along resource ratio gradients according to their relative competitive abilities for the potentially limiting resources was tested using natural communities from Lake Michigan. Algae were grown in six continuous cultures for 46 d on a gradient consisting of four silicon to phosphorus (Si:P) loading ratios: 313:1 (two cultures), 71:1, 4.6:1, and 0.9:1 (two cultures). Diatoms were the superior competitors for P and dominated the three high Si:P ratio cultures at steady state. Green algae dominated the three low Si:P ratio cultures. The two cultures at Si:P = 313 were very similar and were dominated by the diatom *Synedra filiformis*. Stable coexistence was demonstrated at Si:P = 71, where *S. filiformis* and *Diatoma elongatum* co-occurred. The three low Si:P ratio cultures were dominated by a green unicell. Six common species, including the three dominant species, were isolated and tested for their ability to grow under limitation by Si and P. Trade-offs in competitive ability predicted from continuous culture results were confirmed. Species were ranked in competitive ability for Si as follows: the green unicell and the green alga *Monoraphidium contortum* (with no Si requirements) were better than *D. elongatum* and *Asterionella formosa*, which were better than *S. filiformis* and *Fragilaria crotonensis*. The ranking for P was exactly the opposite. Results illustrate that phytoplankton natural community continuous cultures provide a method for evaluating potential changes in community structure resulting from long-term changes in loading ratios of resources.

L'hypothèse voulant que les espèces phytoplanctoniques se répartissent selon les gradients de ressources en fonction du succès de leur compétition pour les ressources limitatives a été testée à l'aide de communautés naturelles du lac Michigan. Des algues ont été cultivées pendant 46 j dans six cultures en continu présentant quatre rapports de teneurs en silicium et phosphore (Si:P) : 313:1 (deux cultures), 71:1, 4,6:1 et 0,9:1 (deux cultures). Les diatomées étaient les meilleurs compétiteurs pour le P et ont dominé, à l'équilibre, les trois cultures à rapports élevés Si:P. Les algues vertes ont dominé les trois cultures à faibles rapports Si:P. Les deux cultures de rapport Si:P de 313:1 étaient très semblables et étaient dominées par la diatomée *Synedra filiformis*. Il y avait coexistence stable dans la culture Si:P de 71:1 où l'on trouvait ensemble *S. filiformis* et *Diatoma elongatum*. Les trois cultures à faibles rapports Si:P étaient dominées par une algue unicellulaire verte. Six espèces courantes, dont les trois espèces dominantes, ont été isolées et l'on a déterminé leur capacité à croître en teneurs limitatives en Si et en P. Le jeu de la compétition indiqué par les résultats des cultures en continu a été confirmé. Les espèces ont été classées par ordre décroissant de succès concernant la compétition pour le Si, comme suit : algue verte unicellulaire et algue verte *Monoraphidium contortum* (aucun besoin de Si), *D. elongatum* et *Asterionella formosa*, et *S. filiformis* et *Fragilaria crotonensis*. L'ordre était exactement inverse pour le P. Ces résultats montrent que les cultures en continu de communautés phytoplanctoniques naturelles permettent d'évaluer les modifications des structures des communautés qui pourraient résulter de changements à long terme du rapport des teneurs en ressources.

Received January 2, 1985
Accepted May 17, 1985
(J8063)

Reçu le 2 janvier 1985
Accepté le 17 mai 1985

The responses of phytoplankton to variable phosphorus supplies in the Great Lakes are complex and multidimensional. Whole lake P addition experiments (Schindler et al. 1978) and lake restoration projects (Edmondson and Lehman 1981) have clearly demonstrated that P loading is the most important factor determining phytoplankton biomass in lakes. Phytoplankton species composition also changes drastically in response to changes in P loading. The role of limiting nutrients in shaping phytoplankton community structure has been reviewed recently by Tilman et al. (1982) and Kilham and Kilham (1984). They concluded that resource competition in addition to other factors is an important mechanism determining spatial and temporal distributions and relative species abundance patterns. Work cited in those reviews has shown that the species are not affected solely by P, but also by other resources, and therefore, resource ratio gradients are important in species interactions. For example, when there is sufficient silicon and nitrogen (high Si:P and N:P ratios), diatoms appear to be good competitors for P (Tilman and Kiesling 1984). How-

[1]This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

ever, green algae gain the advantage over diatoms as Si: demand increases (lower Si:P ratios; Sommer 1983). If N loading decreases relative to P (low N:P ratios), then N-fixing blue-green algae become dominant (Smith 1983). These studies suggest that P dynamics should be studied in relation to the dynamics of other potentially limiting resources if we are to understand mechanisms involved in determining successional phenomena in natural communities.

Our task was to try to understand the specific physiological mechanisms underlying phytoplankton species interactions under resource limitation. Laboratory experiments on unialgal clones of algae with known physiological characteristics have already demonstrated that the outcome of competition experiments can be predicted with a high degree of accuracy (Tilman 1977, 1981; Holm and Armstrong 1981; Kilham 1984). Species can be very different in their abilities to grow under limitation by Si or P, and there appear to be trade-offs in competitive ability, i.e. a species that is very good at growing under limitation by one resource is not very good at using another resource. This allows species to be ranked along resource ratio gradients according to their relative competitive abilities (Tilman et al. 1982).

This article addresses some of the responses of a natural phytoplankton community from Lake Michigan to long-term steady-state differences in loading rates of Si and P. These two resources are both potentially limiting to species in Lake Michigan (Tilman et al. 1984). Instead of starting with unialgal cultures and putting them together in competition, these experiments allow a random suite of species to compete and then the physiological characteristics of the winning species are determined. The experiments were designed to test the hypothesis that phytoplankton species from a natural population will assort themselves along a Si to P supply gradient according to their relative competitive ability, and that the species dominating at steady state will exhibit trade-offs in their relative abilities to grow under limitation by Si and P that will be consistent with their distributions along the Si:P ratio gradient. Other community properties such as species diversity and C:N:P ratios were also determined.

Experimental Design and Methods

The continuous culture system was chosen to minimize the effects of physical variables (temperature, light, sinking, etc.) so that nutrient interactions could be studied with a minimum number of interferences. Water for the inoculum for the continuous cultures was taken from Lake Michigan at the Milwaukee (Wisconsin) water intake system on 26 December 1979 and sent by air to Woods Hole Oceanographic Institute in insulated cartons. The time from lake to cultures was 7 h; temperature at the time of collection and on arrival at the laboratory was 8.5°C. The water sample was dominated by diatoms (*Melosira*, *Fragilaria*, and *Stephanodiscus*) and had a soluble Si:P ratio of 180. Six preautoclaved 500-mL polycarbonte flasks were each filled with 400 mL of whole lake water and placed in the culture box on a rotary shaker (180 rpm for 10 $s \cdot min^{-1}$). Influent medium was WC (Guillard 1975) modified by adding B and with an order of magnitude less Cu and Zn. No buffers or ammonium were added. Nitrate was modified by adding 900 μmol $NaNO_3 \cdot L^{-1}$ and 100 μmol $KNO_3 \cdot L^{-1}$ in order to provide sufficient K to the medium. The four influent Si:P ratios (all units are micromoles per litre) were 4.5 Si : 4.9 P = 0.9 (for the first 22 d, the [P] was 2.5 $\mu mol \cdot L^{-1}$, giving a ratio of 1.8), 46 Si : 10 P = 4.6, 47 Si : 0.66 P = 71, and 97 Si : 0.31 P = 313. Two continuous cultures were supplied with medium at Si:P = 313, two at Si:P = 0.9, and one each at Si:P = 4.6 and 71. The influent medium was sterilized by autoclaving in Teflon bottles and decanted after cooling into sterile polycarbonate 1-L flasks with inverted Tripour beaker covers. Silicone tubing and stoppers were used throughout the apparatus. A Manostat Casette Pump was used to drive the system at 0.25 $\cdot d^{-1}$, i.e. 100 $mL \cdot d^{-1}$ displaced with a culture volume of 400 mL. Each reactor was fitted with a silicone stopper through which stainless steel tubing inflow and outflow ports passed. The inflow port was above the level of the culture and supplied medium in drops. Because the stoppers fit snuggly in the flasks, the pressure of the drops coming in forced an equal volume of the culture out through the outflow port which was located about halfway into the culture medium. The effluent was collected in 250-mL flasks through small holes in the tops of inverted Tripour beakers. The volume of the effluent and the in vivo fluorescence (Turner Designs Fluorometer) were measured daily. Periodic samples were taken directly from the reactors for algal counts and identifications using an inverted microscope. Species diversity calculation (H') were made using $\log_e$ (unit = nat). The entire system was housed in a culture box at 10°C, with light from above at 850 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the flask surface on a 14-h light to 10-h dark cycle. The system ran continuously for 46 d. The reactor flasks were changed every 4–5 d to avoid algal growth on the walls of the flask, and effluent lines were replaced every 6–10 d to prevent clogging.

The relative abilities of these species to grow under limitation by Si or P were determined using a quasi-steady-state large volume batch culture technique. Algae were isolated from the continuous culture reactors from days 10–30 to establish unialgal cultures of the dominant species. Six species were chosen for study: the green unicell (a chlorophyte 4–6 μm in diameter with an uneven cell wall, a clear vacuole space, and a cup-shaped chloroplast), *Monoraphidium contortum* (Thuret in Breb.), *Diatoma elongatum* (Lyngb.) Agardh, *Asterionella formosa* Hass., *Fragilaria crotonensis* Kitton, and *Synedra filiformis* Grun. *Asterionella formosa* was selected because it has been well characterized physiologically (see table 1 in Tilman et al. 1982) although it never became abundant in the cultures. All other species were at least 15% of the total cells in one or more of the cultures during some period of the experiment. Twelve 1-L polycarbonate flasks were filled with 900 mL of modified WC with P and Si omitted. To six flasks, P was added to 50 $\mu mol \cdot L^{-1}$, and Si was added as follows (all units in micromoles per litre): 0.5, 0.6, 1.0, 1.8, 3.7, and 8.1. To another six flasks, Si was added to 100 $\mu mol \cdot L^{-1}$, and P was added as follows (all units in micromoles per litre): 0.04, 0.08, 0.101, 0.24, 2.7, and 4.0 (because of problems with the standards, these values should be considered relative and not absolute). After autoclaving, each flask was inoculated with a very low number of cells (about 1 cell $\cdot mL^{-1}$) of each of the six species. Samples were taken for chemical analyses of Si and P (see Kilham et al. 1977). The cells were allowed to acclimate for 3 d, with the flasks mixed by hand three times each day. Flasks were placed in the culture box used for the continuous culture experiments under the same conditions already described. Starting on day 3, 100-mL samples were decanted from each flask into graduated cylinders and pre-

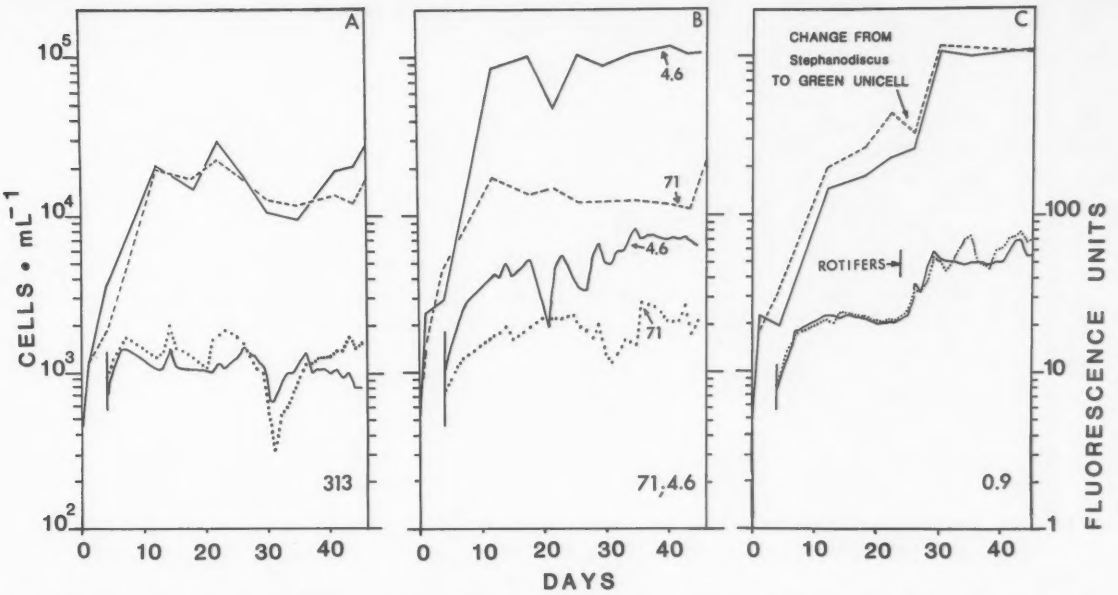


FIG. 1. Cell numbers (upper curves) and biomass as measured by in vivo fluorescence (lower curves) for the six natural community continuous cultures. (A) Two cultures run simultaneously at Si:P = 313; (B) the two cultures run at Si:P = 4.6 (solid line) and Si:P = 71 (broken line); (C) the two cultures run simultaneously at Si:P = 0.9. A twofold increase in P concentration occurred at day 22. Rotifers occurred in all cultures until day 18 and in the two cultures at Si:P = 0.9 until day 26.

served with Lugol's iodine solution. After settling for 24 h, the top 95 mL was drawn off and all of the algae in the remaining 5-mL sample were counted using an inverted microscope. This procedure was repeated daily for 5 d. The growth rates of each species were calculated as the slope of the ln cells per day. The Monod curves of growth rate versus substrate concentration were determined using a nonlinear regression technique (Kilham et al. 1977). Nutrient analyses were performed at the end of the experiment to make certain that the concentrations of the limiting nutrient had not changed more than 10% over the time of the experiment. The equilibrium concentration (R^*) of P or Si at $0.25 \cdot d^{-1}$ was calculated (Tilman 1981) for each species from the Monod relationship ($R^* = 0.25(K)/r - 0.25$, where K is the Monod half saturation constant for growth and r is the maximum growth rate). In this way, the resource limited growth response of each species could be determined under identical conditions, and a ranking as to relative competitive abilities could be established.

The C and N analyses performed by the Chemistry Department at Woods Hole Oceanographic Institution were done on filtered samples taken on the final day of the continuous culture experiments. Filters were precombusted glass fiber filters, and blank filters with distilled water or culture medium passed through were also determined. The particulate P analyses were performed on 20-mL samples collected on Nuclepore filters and measured after digestion (Menzel and Corwin 1965). Results were within 10% of the mass balance calculation of particulate P in all cases.

Results and Discussion

The hypothesis that phytoplankton species from a natural population will assort themselves along a Si to P supply gradient, and that the species dominating at steady state will exhibit trade-offs in their relative abilities to grow under Si and P limitation consistent with their distributions along that gradient, was generally confirmed by the experiments. The results of the long-term natural community continuous cultures demonstrated many of the predictions of resource competition theory (Tilman 1982). There were only as many dominant species at steady state as there were potentially limiting resources (one or two). The phytoplankton species that dominated at steady state showed trade-offs in their abilities to grow under Si and P limitation consistent with their positions on the Si:P ratio gradient. The species diversity decreased with increasing resource richness, with the smallest effect at intermediate additions of both Si and P. The C:N:P stoichiometric relationships of the dominant steady-state communities were very different and showed that diatoms have a lower requirement for P than do green algae.

Dynamics of the Continuous Cultures

All of the phytoplankton natural community continuous cultures approached a steady state in species composition by about days 30–35. Cell numbers and biomass approached steady-state values in all of the cultures in about 10 d (Fig. 1). The two cultures run simultaneously at the lowest Si:P ratio (Fig. 1C) had a twofold change in the influent concentration of P on day 22 (Si:P ratio changed from 1.8 to 0.9) which resulted in an increase in cell numbers and fluorescence in about 5 d to new steady-state values in both cultures. This was a clear demonstration that the phytoplankton community was P limited. The changes in species composition at the same time may have been the result of changing the Si:P supply ratio. Generally, the fluorescence and cell numbers increased with increasing P concentrations, except for the culture with the highest P supply

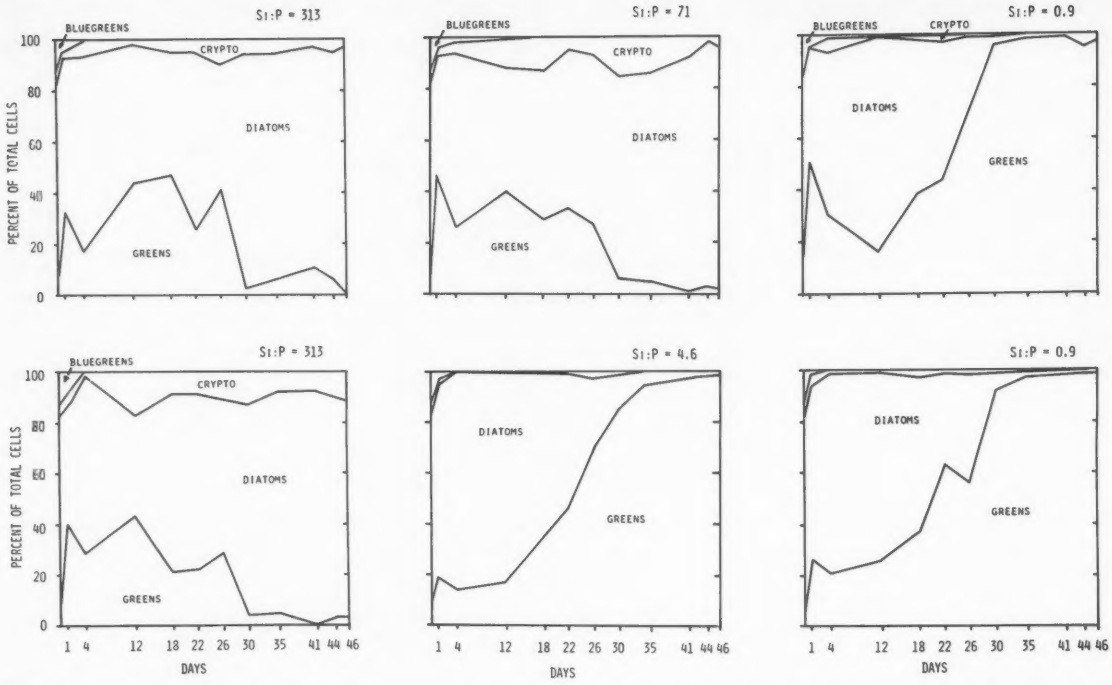


FIG. 2. Dynamics of changes in phytoplankton community structure in the six continuous cultures. The three cultures with high Si:P ratios (313, 71) were similar in their dynamics, as were the three cultures at low Si:P ratios (4.6, 0.9).

(Si:P = 4.6, P = 10.0 μmol·L^{-1}), which had values that were not significantly different from those cultures that had P concentrations of 4.9 μmol·L^{-1} (Si:P = 0.9, compare curves in Fig. 1B and 1C). Possibly the high P concentration being supplied to the Si:P = 4.6 culture resulted in light limitation or limitation by some other resource. There was measurable phosphate remaining in the reactor at the end of the experiment (0.4 μmol·L^{-1}), although this was very close to the predicted R^* value for the green unicell which dominated the culture (see later discussion). In Fig. 1A, the abrupt decrease in fluorescence and cell numbers in the two Si:P = 313 cultures was caused by a "bad" batch of medium which might have had some essential element omitted; replacing the influent medium solved the problem very quickly. All of the cultures had rotifers in them on day 18, but only the two cultures at Si:P = 0.9 had them on day 22. They were absent from all cultures on day 26. Ciliate protozoans were also present in all of the cultures, but never in high abundance. In the cases where two duplicate continuous cultures were being supplied from the same influent reservoir (Fig. 1A and 1C), the results for the replicates were very consistent in fluorescence and cell numbers. This demonstrates the replicability of the technique and also that the outcome of the species interactions was controlled by the influent medium.

Changes in the phytoplankton community structure over the course of the experiment for the six cultures are illustrated in Fig. 2. The results indicate that diatoms are superior competitors for P, but are replaced by green algae as the relative supply rates of Si decrease relative to P. Diatoms dominated in the three cultures with the highest Si:P ratios (313 and 71), and green algae dominated in the three cultures with the lowest Si:P ratios (4.6 and 0.9). Blue-green algae were eliminated very early in all of the cultures (N:P ratios were always above 100:1). Cryptomonads remained in all of the cultures, but were relatively more abundant in the high Si:P ratio cultures than in the low ratio cultures. Sommer (1983) demonstrated a similar shift in phytoplankton community structure for natural community continuous cultures from Lake Constance (Germany) over a Si:P ratio gradient of 4:1 to 80:1.

One of the major predictions of resource competition theory (Tilman 1982) is that there should only be as many dominant species as there are limiting resources at steady state. In five of the cultures, one species dominated, and in one culture two species coexisted. The dynamics of the dominant species over the 46 d are shown in Fig. 3. The duplicate cultures (5 and 6) with a Si:P supply of 313 (the most P-limited case) became dominated by *S. filiformis* which reached 90% of the total cell numbers. Because of its large size, it dominated phytoplankton biomass to an even greater extent. Other workers studying the effect of P limitation in natural phytoplankton continuous cultures have also found that some species of *Synedra* dominated in the most P-limiting case (Sommer 1983; Smith and Kalff 1983; Tilman and Kiesling 1984). Tilman (1981) and Kilham (1984) have shown that *Synedra* species have the lowest growth requirements for P of any species tested, and the highest requirements for Si. This "trade-off" in competitive ability for two potentially limiting resources (see Tilman et al. 1982) means that *Synedra* should be replaced by another species as the Si:P ratio decreases because its growth becomes limited by Si. This is in fact what happened at a Si:P ratio of 71, where *S. filiformis* stably coexisted with *D. elongatum* as codominants. The published values for the P and Si growth kinetics of

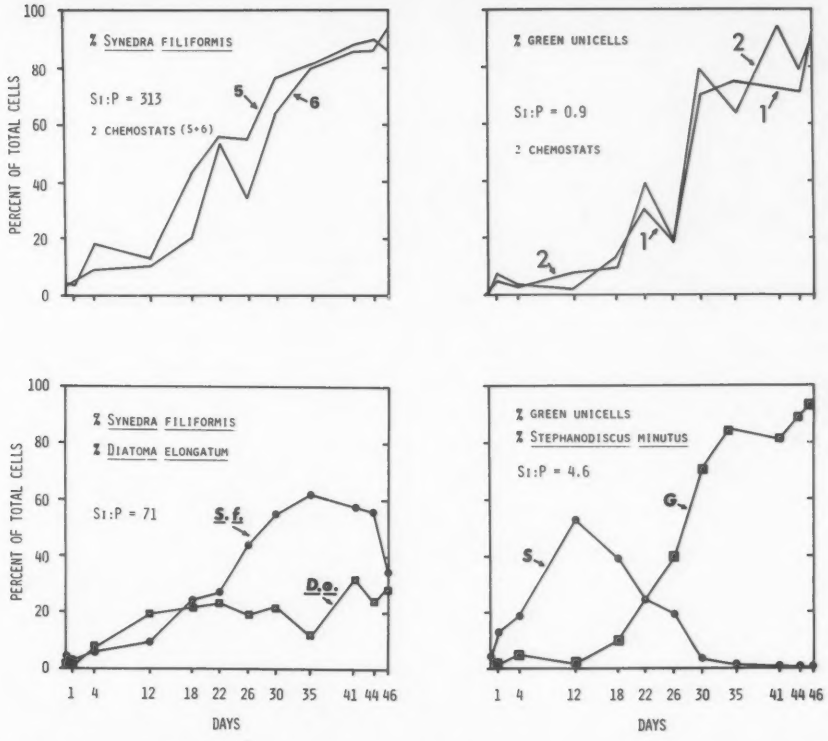


FIG. 3. Dynamics of the dominant species in each of the continuous cultures at the four influent Si:P ratios. The two cultures (5 and 6) at Si:P = 313 were dominated by *S. filiformis*. The two cultures (1 and 2) at Si:P = 0.9 were dominated by the green unicell. In the Si:P = 71 culture, two species stably coexisted, *S. filiformis* (S.f.) and *D. elongatum* (D.e.). In the culture at Si:P = 4.6, one species (*S. minutus*; S) was replaced by the green unicell (G).

D. elongatum (Kilham et al. 1977) are consistent with an interpretation of Si limitation for *Synedra* and P limitation for *Diatoma* in the Si:P = 71 case. In the three lowest Si:P ratio cultures, the dominant species was the unidentified green unicell. In the duplicate cultures at Si:P = 0.9, the dynamics of approach to steady state were similar, and on the last day this species was 90% of the total cells in both cultures. In the culture at Si:P = 4.6, there was an early dominance by a small diatom, *Stephanodiscus minutus*, which was replaced by the green unicell after day 22.

The dynamics of abundance of common species that did not become the final dominants are shown in Fig. 4. The replacement of the diatom *S. minutus* by the green unicell was also observed in the Si:P = 0.9 duplicate cultures (1 and 2 in Fig. 4). These cultures had an influent Si:P ratio of 1.8 until day 22, at which time it was changed to Si:P = 0.9. The change in dominance was later (days 26–30) than in the Si:P = 4.6 culture. Kilham (1984) showed that another clone of *S. minutus* from Lake Michigan had an optimum Si:P ratio of 1.0 at 10°C. The growth behavior of this species in all of the cultures was indicative of its having a growth optimum at low Si:P ratios, because its relative abundance and longevity in the cultures increased with decreasing Si:P ratios. However, the question can be asked of why *S. minutus* did not stably coexist with the green unicell, with the abundance of *S. minutus* determined by the silicate concentration, as might be expected if this species had an optimum Si:P ratio of about 1.0. There was residual Si in the reactors at Si:P of 4.6 and 0.9 that could have supported additional growth by *S. minutus*. This question cannot be answered within the scope of this experiment. An attempt was made using unialgal cultures to determine if the green unicell produced a substance that inhibited the growth of *S. minutus*, but no such affect was observed under nutrient-sufficient conditions (S. Kilham, unpubl. data). Another possibility is that the pH of the denser cultures increased to a point that inhibited the growth of *S. minutus* (pH was not measured in the reactors; the influent medium had a pH of 7.5). The pH of subsequent cultures that were 10 times the biomass of the highest ones in these experiments rarely exceeded 8.0. Calculations indicate that dissolved inorganic carbon is unlikely to be limiting (Novak and Brune 1985).

Two species of green algae, *M. contortum* and *Ankistrodesmus* sp., were essentially eliminated from the high Si:P ratio cultures by day 30 (with the exception of a short-lived resurgence of *M. contortum* in culture 5 at Si:P = 313; Fig. 4). *Ankistrodesmus* sp. did appear to stably coexist with the green unicell in the three low Si:P ratio cultures. Two diatom species, *F. crotonensis* and *Fragilaria* sp., became more abundant at the end of the experiment at Si:P = 71. It was observed on day 46 that they were sticking to the walls of the reactor flask, which had last been replaced on day 41. The decreased morality rate caused by avoidance of the effluent could account for

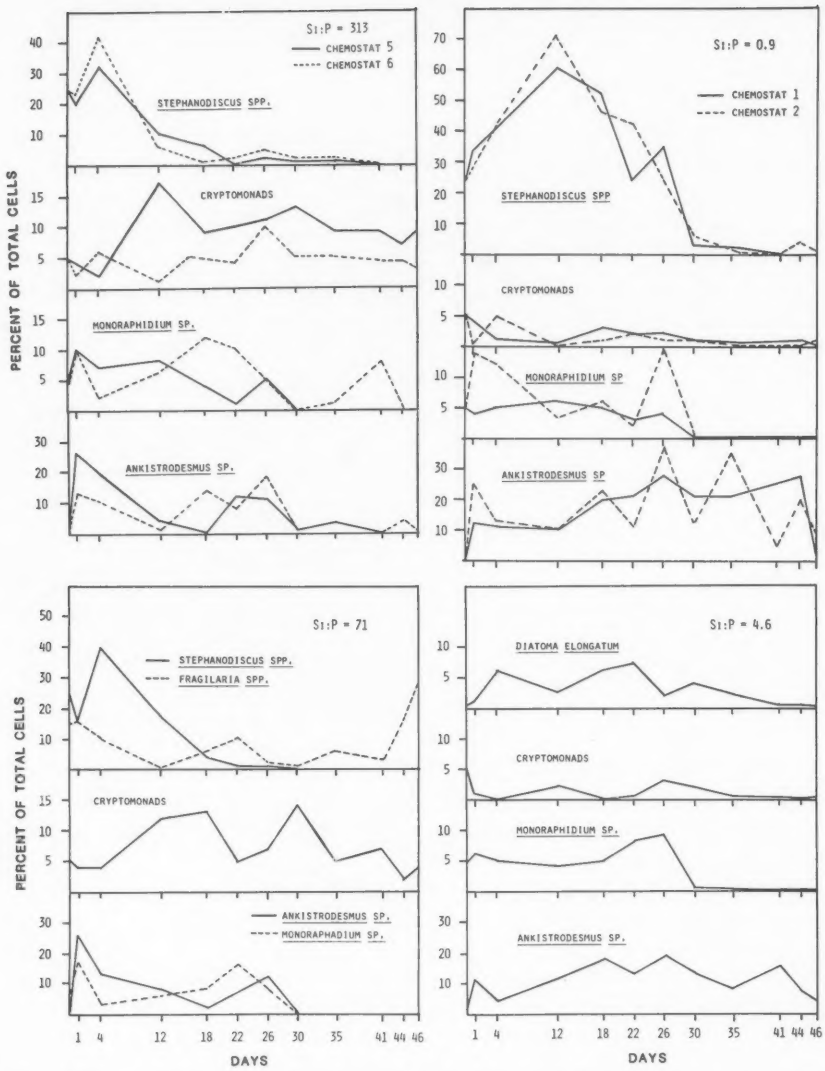


FIG. 4. Dynamics of the species that were at least 5% of the total cell numbers during some period of the experiment. The two cultures at Si:P = 313 (5 and 6) and 0.9 (1 and 2) are the same as in Fig. 3.

the apparent increase in these two species. The optimum Si:P ratio for *F. crotonesis* is intermediate between *Synedra* and *Diatoma* (see Tilman et al. 1982) and this could account for its increasing abundance, which was at the expense of *S. filiformis* and not *D. elongatum* (Fig. 3). Possibly, *Fragilaria* could have replaced *Synedra* as the codominant with *Diatoma* at Si:P = 71 if the experiment had been continued for a longer period, which would have been more consistent with the known resource physiology of these three species. In the unialgal culture experiments discussed later, it was not possible to distinguish between *F. crotonensis* and *S. filiformis* in either their P or Si growth requirements. Crytomonad species appeared to stably coexist with the diatoms at the higher Si:P ratios (Fig. 4), with abundances of 5−10% of the total cells. Their small size relative to the dominant diatoms meant that their contribution to the biomass of the cultures was less than 1%. Because virtually nothing is known about the resource-limited growth requirements of cryptomonads in the Great Lakes, it is difficult to make any interpretation of their apparent stable co-occurrence in the cultures.

C:N:P Cellular Stoichiometry

The measurement of elemental C:N:P ratios in phytoplankton has been used by a few investigators to estimate the nutritional status of populations (Sakshaug and Holm-Hansen 1977; Jones et al. 1978). Healey and Hendzel (1980) found a very good relationship between the N:P ratio in the phytoplankton

TABLE 1. C:N:P atomic ratios for phytoplankton communities in the six continuous cultures on the final day (day 46) of the natural community experiments. Influent nitrate concentration was 1000 $\mu mol \cdot L^{-1}$ in all cultures.

Influent Si:P	C:N:P	C:N
0.9	39:5.6:1	7.0
0.9	54:9.8:1	5.5
4.6	27:4.8:1	5.7
71	233:32 :1	7.4
313	326:38 :1	8.6
313	396:50 :1	7.9

and the N:P loading ratios to the lakes they studied. It may be possible to use the C:N:P ratios of the phytoplankton as an indicator of the type and degree of resource limitation in the Great Lakes.

At the end of the experiment the C, N, and P contents of the algae from the cultures were measured and the C:N:P ratio calculated (Table 1). Because neither C nor N were limiting, one expects that the C:N ratio would approximate the Redfield atomic ratio of 6.6. The C:N ratio averaged 7.0 for all six cultures, with the three cultures dominated by the green unicell (Si:P = 0.9, 4.6) having a somewhat lower value of 6.1 and the three cultures dominated by the araphid diatoms (Si:P = 71, 313) having a higher value of 8.0. The C:P and N:P ratios of the six cultures were strikingly different. None of the cultures approximated the Redfield ratio of 106 C : 16 N : 1 P. The three cultures dominated by the green unicell had C:N:P ratios that averaged 40:7:1, and the three cultures dominated by araphid datoms had ratios that averaged 318:40:1. These data indicate that the diatoms had a much lower cellular requirement for P than did the green unicell, and are consistent with the conclusion that diatoms are superior competitors for P. Data from Lake Erie indicate that the algae have C:N:P ratios relatively close to the Redfield ratio, with Burns and Ross (1972) reporting 122 C : 18 N : 1 P and Leach (1981) reporting 126 C : 19 N : 1 P. This could mean that the algae are not growth rate limited by N or P. Perhaps light or some other elements are important resources in Lake Erie. The mean value for all stations in southern Lake Michigan in 1976 was 800 C : 55 N : 1 P (Bartone and Schelske 1982), which indicates P limitation of the phytoplankton and dominance by diatoms. There are amazingly few data available on the cellular elemental stoichiometry of the phytoplankton in the Great Lakes, so conclusions are only tentative.

Batch Culture Kinetic Experiments

Part of the hypothesis tested was that the species dominating at steady state will exhibit trade-offs in their relative abilities to grow under Si and P limitation (Tilman 1982; Tilman et al. 1982). The hypothesis was tested on unialgal clones of six species isolated from the continuous cultures during the course of the experiment. The equilibrium resource concentration, R^* (Tilman 1981), was calculated from the measured Monod relationships for P and Si for each species at the growh rate of $0.25 \cdot d^{-1}$ (the flow rate of the continuous cultures; Table 2). Based on the outcome of the continuous cultures, one would predict that the green unicell would have the lowest requirement for Si and the highest requirement for P, that *S. filiformis* would have the highest requirement for Si and the lowest requirement for P, and that *D. elongatum* should be intermediate between these two species. These predictions were confirmed by the unialgal culture studies (Table 2). Green algae have no requirement for Si, but their requirements for P are an order of magnitude higher than those of the diatoms. *Diatoma elongatum* and *A. formosa* were intermediate in their requirements for both nutrients, and *S. filiformis* and *F. crotonensis* had the highest requirements for Si and the lowest requirements for P (in fact, both of these species grew at maximum growth rates at the lowest P concentration of 0.04 $\mu mol \cdot L^{-1}$).

TABLE 2. Calculated R^* values at a growth rate of $0.25 \cdot d^{-1}$ for P (P*) and Si (Si*) for six species isolated from Lake Michigan natural community continuous cultures at 10°C.

Species	P* ($\mu mol \cdot L^{-1}$)	Si* ($\mu mol \cdot L^{-1}$)
Green unicell	0.34	0
Monoraphidium contortum	0.19	0
Diatoma elongatum	0.035	0.27
Asterionella formosa	0.036	0.34
Synedra filiformis	<0.02[a]	0.73
Fragilaria crotonensis	<0.02[a]	0.90

[a]These are maximum values; these two species were growing at maximum growth rate at 0.04 $\mu mol\ P \cdot L^{-1}$.

The large volume batch culture technique has the advantage that the growth rates of each species are measured in exactly the same nutrient environment. However, only six different nutrient concentrations were used to determine the Monod curves from which the R^* values for each resource were calculated, so large confidence intervals are associated with the calculations. The relative position of the R^* values for each species is a better index of competitive ability than the absolute value of P* or Si*. Results such as those in Table 2, with differences of 2- to 10-fold in the R^* values, are clear and certainly adequate for drawing conclusions about the relative competitive abilities for species in this case because of the large nutrient supply gradients (20 times for Si, 30 times for P, and 350 times for Si:P). The relative rankings of the Si* and P* values for other clones of the four diatom species from Lake Michigan are quite comparable with those calculated from published data (Table 3), although those experiments were all performed at 20°C, and temperature effects on nutrients kinetics have been documented for some of these species (Tilman et al. 1981; Kilham 1984).

Species Diversity

One of the predicted responses of a plant community to increased resource supply is that species diversity should decrease (Tilman 1982). The Shannon–Wiener diversity index (H') decreased in all cases (Table 4) over the course of the continuous culture experiments, with the greatest decreases at the extremes of Si and P additions, and the least effect observed for moderate additions of both nutrients (Si:P = 71). This effect was predicted theoretically by Tilman (1982). Relatively high diversity was maintained for the first 18 d of the experiment, but then declined as the species that were eventually competitively dominant became more abundant. In lakes, changes in supply rates of resources are likely to be more gradual and continuous rather than abrupt as in experimental situations, so species diversity can remain relatively high as dominance changes occur. There is also some degree of vari-

TABLE 3. Calculated R^* values at a growth rate of $0.25 \cdot d^{-1}$ for P (P*) and Si (Si*) for diatoms isolated from Lake Michigan. All experiments were performed at 20°C.

Species	P* ($\mu mol \cdot L^{-1}$)	Si* ($\mu mol \cdot L^{-1}$)	Reference
Diatoma elongatum	0.022	0.63	Kilham et al. 1977
Asterionella formosa	0.004	1.04	Tilman 1981
	0.042	1.30	Holm and Armstrong 1981
Fragilaria crotonensis	0.005	1.01	Tilman 1981
Synedra sp.	0.009	1.6, 1.2	Kilham 1984
Synedra filiformis	0.002	5.79	Tilman 1981

ability associated with resource supply rates in lakes which can lead to a higher diversity of stably coexisting species (Tilman 1982; Sommer 1984).

Long-Term Experiments: Ecological Implications

If phytoplankton species distribute themselves along resource ratio gradients using relative competitive abilities as the mechanism, as these and other experiments suggest (Sommer 1983; Tilman and Kiesling 1984), then there are implications for the interpretation of natural community bioassay experiments (Kilham and Kilham 1978). In any particular water sample, the dominant species would be those whose resource growth requirements most closely resemble the relative supply rates of the potentially limiting resources. In bioassay experiments, usually one nutrient at a time is added or all nutrients but one are added. In either case, the ratio gradients are shifted drastically away from "optimum" supply rates for the dominant species. For example, if a water sample contained species that had been supplied Si and P in a ratio of 100:1 and only P were added, the ratio would shift down and Si demand would increase. The dominant species of diatoms would become growth limited by Si, and the rarer species that had lower (or no) Si requirements would find themselves with a growth advantage and would increase. However, if all nutrients except P were added, the species with a higher Si requirement, but lower P requirement, would increase until they became P limited. In either case, species with higher growth rates would have the short-term advantage. Short-term batch culture bioassay experiments are likely to exhibit responses that are quite different from longer term continuous culture experiments. The species that become dominant early in natural community continuous culture experiments are not necessarily the competitive dominants at the end of the experiments (Fig. 3 and 4; Sommer 1983; Smith and Kalff 1983). Thus, bioassay experiments may be sufficient for determining that certain resources are potentially limiting to the algal species present, but they are usually inadequate for predicting the eventual species or even community responses that would be a consequence of long-term changes in resource supply. Natural community continuous cultures provide a method for investigating the potential for species and community changes resulting from long-term changes in supply rates of resources. Modifications of design would be useful for investigating such complications as species-specific mortality owing to factors such as grazing (Lehman and Sandgren 1985). Species-specific grazing can lead to changes in competitive dominance because of the increased resource demand of the affected species to maintain growth rates high enough to offset increased loss rates. There are a large number of other species-specific responses that are not considered in such controlled laboratory situations, such as mechanisms that minimize losses or resistance to parasitism, that can complicate any extrapolation of results to specific lake situations (see Reynolds 1984).

TABLE 4. Shannon–Wiener diversity index (H') for each of the natural community continuous cultures. The original samples used as the common inoculum had $H' = 1.04$.

Si:P	Day 18	Day 35	Day 46
0.9	0.82	0.32	0.10
0.9	0.88	0.33	0.19
4.6	0.81	0.28	0.12
71	0.84	0.50	0.61
313	0.85	0.35	0.24
313	0.94	0.37	0.15

The natural community experiments emphasize that knowing the supply rates of only one resource such as P does not provide enough information for making informed judgements about potential changes in phytoplankton community structure (Kilham and Kilham 1984). It is necessary to know something about the loading rates of other potentially limiting resources especially when P loading is variable. For the Great Lakes, one of those resources is Si. Kilham (1971) proposed that Si demand should increase with increased eutrophication, and Schelske et al. (1983) have attempted to quantify this increased Si demand in sediments in the Great Lakes. The competitive interactions of diatom species based on trade-offs in the ability to grow under limitation by Si and P provide a mechanism for explaining the observed changes in the Si budget. Diatom species in the sediment cores studied by Schelske et al. (1983) should change as the relative loadings of Si and P to the lake change, with araphid diatoms such as *Asterionella* and *Fragilaria* being replaced by small centric diatoms such as *Stephanodiscus* and *Cyclotella* as Si demand increases (Si:P loading ratio decreases). One attempt to test the applicability of predicted diatom species distributions in the Great Lakes based on competitive abilities was discussed in detail by Tilman et al. (1984). It would clearly be desirable to have more field tests of the relative importance of competitive interactions and other factors important to phytoplankton.

The turnover (flow) rate of the continuous cultures ($0.25 \cdot d^{-1}$) was chosen as being representative of the turnover rates encountered in Lake Michigan. In 1983, for example, the average chlorophyll turnover rate over the summer in southern Lake Michigan was $0.2 \cdot d^{-1}$ (J. Lehman, Division of Biological Sciences, University of Michigan, Ann Arbor, MI 49109-1048, and D. Scavia, G.L.E.R.L., NOAA, Ann Arbor, MI 48104,

pers. comm.). Sommer (1983) and Tilman and Kiesling (1984) also chose similar turnover rates for their natural community experiments. There is some indication that the turnover rate chosen can affect the resulting phytoplankton species composition, even with constant resource supply ratios (Smith and Kalff 1983; Sommer and Kilham 1985). This is likely to be particularly important for species with very low or very high maximum growth rates.

The natural community continuous culture experiments reported here were used in an attempt to bridge the gap between controlled laboratory experiments and phytoplankton interactions in lakes. Some control is obviously necessary to elucidate mechanisms involved in species interactions, but using random phytoplankton populations from nature brings a higher degree of potential complexity to the experiments. The natural community experiments are the reverse experiments to those performed using unialgal cultures where the nutrient growth kinetics of each species are determined and used to predict the outcome when they are put together in competition (Tilman 1977, 1981; Tilman et al. 1981; Holm and Armstrong 1981; Kilham 1984). In the natural community experiments, the random population of algae is allowed to compete until a steady state is achieved. Then the prediction (Tilman 1982) of species differences in competitive ability for the potentially limiting nutrients is tested by measuring the nutrient growth kinetics of the dominant species. For the experiments reported here, the predictions were confirmed by the unialgal Monod experiments (Table 2). Although other workers performing natural community experiments did not test for trade-offs, the results in terms of phytoplankton community structure were remarkably similar to those reported here, with diatoms dominating at high Si:P ratios and green algae dominating at low Si:P ratios (Sommer 1983 for Lake Constance, West Germany; Tilman and Kiesling 1984 for Lake Superior, United States). Furthermore, in all cases, some species of *Synedra* dominated the most P-limiting cases (see also Smith and Kalff 1983 for Lake Memphremagog, Canada). The repeatability for natural community experiments, both within an experiment as reported here and between laboratories in three different countries, is quite astonishing and leads one to the conclusion that competitive interactions can be an important factor in determining species and community responses to changes in nutrient loading to lakes.

Acknowledgments

The research was supported by National Science Foundation grants OCE78-27016 and OCE81-17377 to S. S. Kilham and P. Kilham. My very grateful thanks to R. R. L. Guillard who provided space, advice, and encouragement at Woods Hole Oceanographic Institution during my sabbatical in 1979–80. M. Boraas arranged for shipment of water from Milwaukee, and the C. Hoffman family transported it to Woods Hole, MA. R. Dorazio kindly wrote a program for calculating the species diversity. The Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI 48104, provided partial travel support to the Phosphorus–Plankton Dynamics Symposium and publication costs. I thank P. Kilham for advice and encouragement throughout this project. P. Kilham and S. Tarapchak made helpful comments on this manuscript.

References

BARTONE, C. R., AND C. L. SCHELSKE. 1982. Lake-wide seasonal changes in limnological conditions in Lake Michigan in 1976. J. Great Lakes Res. 8: 413–427.

BURNS, N. M., AND C. ROSS. 1972. Oxygen–nutrient relationships within the central basin of Lake Erie, p. 85–119. *In* N. M. Burns and C. Ross [ed.] Project HYPO. Canada Centre for Inland Waters Paper No. 6.

EDMONDSON, W. T., AND J. T. LEHMAN. 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26: 1–29.

GUILLARD, R. R. L. 1975. Culture of phytoplankton for feeding marine invertebrates, p. 29–60. *In* W. L. Smith and M. H. Chanley [ed.] Culture of marine invertebrates. Plenum, New York, NY.

HEALEY, F. P., AND L. L. HENDZEL. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442–453.

HOLM, N. P., AND D. E. ARMSTRONG. 1981. Role of nutrient limitation and competition in controlling the populations of *Asterionella formosa* and *Microcystis aeruginosa* in semicontinuous culture. Limnol Oceanogr. 26: 622–634.

JONES, K. L., P. TETT, A. C. WALLIS, AND B. J. B. WOOD. 1978. Investigation of a nutrient–growth model using a continuous culture of natural phytoplankton. J. Mar. Biol. Assoc. U.K. 58: 923–941.

KILHAM, P. 1971. A hypothesis concerning silica and the freshwater planktonic diatoms. Limnol. Oceanogr. 16: 10–18.

KILHAM, S. S. 1984. Silicon and phosphorus growth kinetics and competitive interactions between *Stephanodiscus minutus* and *Synedra* sp. Verh. Int. Ver. Limnol. 22: 435–439.

KILHAM, S. S., AND P. KILHAM. 1978. Natural community bioassays: predictions of results based on nutrient physiology and competition. Verh. Int. Ver. Limnol. 20: 68–74.

1984. The importance of resource supply rates in determining phytoplankton community structure, p. 7–27. *In* D. G. Meyers and J. R. Strickler [ed.] Trophic interactions within aquatic ecosystems. AAAS Selected Symposium 85, Washington, DC.

KILHAM, S. S., C. L. KOTT, AND D. TILMAN. 1977. Phosphate and silicate kinetics for the Lake Michigan diatom *Diatoma elongatum*. J. Great Lakes Res. 3: 93–99.

LEACH, J. H. 1981. Comparative limnology of inner Long Point Bay, Lake Erie, and adjacent waters of the outer bay. J. Great Lakes Res. 7: 123–129.

LEHMAN, J. T., AND C. D. SANDGREN. 1985. Species-specific rates of growth and grazing loss among freshwater algae. Limnol. Oceanogr. 30: 34–46.

MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

NOVAK, J. T., AND D. E. BRUNE. 1985. Inorganic carbon limited growth kinetics of some freshwater algae. Water Res. 19: 215–225.

REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, Cambridge. 384 p.

SAKSHAUG, E., AND O. HOLM-HANSEN. 1977. Chemical composition of *Skeletonema costatum* (Grev.) Cleve and *Pavlova* (*Monochrysis*) *lutheri* (Droop) Green as a function of nitrate, phosphate, and iron-limited growth. J. Exp. Mar. Biol. Ecol. 29: 1–34.

SCHELSKE, C. L., E. F. STOERMER, D. J. CONLEY, J. A. ROBBINGS, AND R. M. GLOVER. 1983. Early eutrophication in the lower Great Lakes: new evidence from biogenic silica in sediments. Science (Wash., DC) 222: 320–322.

SCHINDLER, D. W., E. J. FEE, AND T. RUSZCZYNSKI. 1978. Phosphorus input and its consequences for phytoplankton standing crop in the Experimental Lakes Area and similar lakes. J. Fish. Res. Board Can. 35: 190–196.

SMITH, R. E., AND J. KALFF. 1983. Competition for phosphorus among co-occurring freshwater phytoplankton. Limnol. Oceanogr. 28: 448–464.

SMITH, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science (Wash., DC) 221: 669–671.

SOMMER, U. 1983. Nutrient competition between phytoplankton species in multispecies chemostat experiments. Arch. Hydrobiol. 96: 399–416.

1984. The paradox of the plankton: fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnol. Oceanogr. 29: 633–636.

SOMMER, U., AND S. S. KILHAM. 1985. Phytoplankton natural community experiments: a reinterpretation. Limnol. Oceanogr. 30: 438–442.

TILMAN, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58: 338–348.

1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62: 802–815.

1982. Resource competition and community structure. Princeton University Press, Princeton, NJ. 296 p.

TILMAN, D., AND R. L. KIESLING. 1984. Freshwater algal ecology: taxonomic trade-offs in the temperature dependence of nutrient competitive abilities,

p. 314–319. *In* M. J. Klug and C. A. Reddy [ed.] Current perspectives in microbial ecology. American Society for Microbiology, Washington, DC.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372.

1984. A reply to Sell, Carney, and Fahnenstiel. Ecology 65: 328–332.

TILMAN, D., M. MATTSON, AND S. LANGER. 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnol. Oceanogr. 26: 1020–1033.

Phosphorus Regeneration by the Predatory Copepod *Diacyclops thomasi*[1,2]

James A. Bowers

Great Lakes and Marine Waters Center, The University of Michigan, Ann Arbor, MI 48109, USA

Bowers, J. A. 1986. Phosphorus regeneration by the predatory copepod *Diacyclops thomasi*. Can. J. Fish. Aquat. Sci. 43: 361–365.

The effects of temperature, prey density, and hunger state on phosphorus regeneration rates of the predatory copepod *Diacyclops thomasi* were estimated while they fed on the limnetic rotifer *Synchaeta pectinata*. Regeneration rates increased linearly from 2.0 to 7.0 nmol P·mg dry $wt^{-1}·h^{-1}$ over a temperature range of 5–20°C. When offered a prey density range of 100–500·L^{-1}, satiated *Diacyclops* increased their regeneration rates to a maximum of 5.0 nmol P·mg dry $wt^{-1}·h^{-1}$. Given the same prey density range, starved *Diacyclops* had regeneration rates that increased to a maximum rate of 8.0 nmol P·mg dry $wt^{-1}·h^{-1}$. Predation rates were in all cases directly proportional to regeneration rates. Although a predator, *Diacyclops* regenerates phosphorus at rates within the ranges of many herbivorous zooplankton species.

L'incidence de la température, de la densité des proies et de l'état d'inanition sur les taux de régénération du phosphore chez le copépode prédateur *Diacyclops thomasi* a été calculée pendant qu'il se nourrissait du rotifère limnétique *Synchaeta pectinata*. Les taux de régénération ont augmenté linéairement de 2,0 à 7,0 nmol P·mg poids $sec^{-1}·h^{-1}$ quand la température variait de 5 à 20°C. Des *Diacyclops* rassasiés ont accru leurs taux de régénération à un maximum de 5,0 nmol P·mg poids $sec^{-1}·h^{-1}$ en présence d'une densité de proies variant de 100 à 500·L^{-1}, densité à laquelle des *Diacyclops* affamés ont atteint un taux maximum de 8,0 nmol P·mg poids $sec^{-1}·h^{-1}$. Dans tous les cas, les taux de prédation étaient directement proportionnels aux taux de régénération. Cependant, un prédateur, *Diacyclops*, regénère le phosphore à des taux semblables à de nombreuses espèces de zooplancton herbivore.

Received November 2, 1984
Accepted May 28, 1985
(J8002)

Reçu le 2 novembre 1984
Accepté le 28 mai 1985

Nutrient regeneration by zooplankton is an important source of phosphorus and nitrogen for phytoplankton growth and reproduction, especially in pelagic communities where outside nutrient supply rates are relatively low (Lehman 1980a; Korstad 1983). Furthermore, differential zooplankton nutrient regeneration quantitatively and qualitatively affects phytoplankton species composition and seasonal succession through algal nutrient competition (Lehman 1980b). Regeneration processes by herbivorous species have received the most attention because of their direct predator–prey relationship with algae. Field and laboratory studies indicate that body weight (Johannes 1964, Ganf and Blazka 1974; Ferrante 1976), phytoplankton density (Martin 1968; Peters 1972; Peters and Rigler 1973; Takahashi and Ikeda 1975), and temperature (Barlow and Bishop 1965; Hargrave and Geen 1968; Jawed 1969; Taguchi 1976; Ferrante 1976) all significantly affect zooplankton nutrient regeneration rates.

Although field experiments with the natural zooplankton assemblage have included predatory species (Ferrante 1976; Lehman 1980a; Korstad 1983), studies on individual species with zooplankton prey have not been performed. Yet in some freshwater pelagic communities such as the Laurentian Great Lakes, predatory copepods are the most numerically abundant zooplankters throughout the year (Torke 1975; Wells 1960; Watson and Carpenter 1974) and sometimes have abundance peaks during the summer months (Gannon 1972; Carter 1969; Wilson and Roff 1973) when phosphorus limits algal production.

The purpose of this laboratory study was to estimate the phosphorus regeneration rates of *Diacyclops thomasi* (Balcer et al. 1984), a predaceous cyclopoid copepod, while it fed on a "preferred" prey, the soft-bodied rotifer *Synchaeta pectinata*. I chose *Diacyclops* because it is the principal copepod predator in Lake Michigan (Torke 1975) and its feeding behavior is well understood (Stemberger 1982). Assuming regeneration was closely linked to feeding, the experiments sought to correlate phosphorus regeneration rates to temperature, prey density, and predator hunger state.

Materials and Methods

A stock culture of *Diacyclops* was initiated from net tow collections in Lake Michigan. The animals were cultured in WC medium (Guillard 1975) at 15°C on a 16:8 light:dark photoperiod. *Cryptomonas erosa* var. *reflexa* was used to feed the naupliar stages and the first three copepodid instars which are herbivorous. Dr. R. S. Stemberger (Dartmouth College,

[1] This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

[2] Great Lakes Research Division Contribution No. 415.

Hanover, NH) kindly provided the *Cryptomonas* culture. *Synchaeta pectinata* was an ideal prey choice for *Diacyclops* because it is soft-bodied, small, and lacks any effective swimming escape response (Stemberger 1982). Mean dry weight (DW) estimates of adult *Diacyclops* females were taken from annual mean weight estimates of Hawkins and Evans (1979).

Phosphorus estimates were calculated from Whatman GF/F filtrate absorbances on a spectrophotometer using 10-cm pathlength cells. Soluble reactive phosphorus (SRP) was analyzed according to Strickland and Parsons (1972), while total dissolved phosphorus (TDP) was analyzed according to Menzel and Corwin (1965).

The basic design to estimate *Diacyclops* regeneration rates was patterned after Stemberger's (1982) experiments. His observations indicated that *Diacyclops* predation was a discontinuous process with ingestion rates dependent on gut fullness, prey packing in the gut, a swimming speed inversely proportional to gut fullness, and prey density. The cyclopoid maximized its prey ingestion rate by adjusting its swimming speed and thus prey-encounter frequencies.

My technique consisted of triplicate control beakers containing a chosen *Synchaeta* prey density to compensate for their own phosphorus excretion. During an experiment, these animals excreted phosphorus at a low and constant rate. Triplicate beakers having the same prey density plus the *Diacyclops* predator served as the experimental treatments. Before initiating any single experiment, the rotifers and cyclopoids were washed in WC medium lacking phosphorus by repeated rinsings in a polyethylene beaker having a 100-μm netting window and submerged in a much larger beaker containing phosphorus-free WC medium. All of the experiments were performed in this phosphorus-free WC medium. Incubation periods had to be long enough to measure predation and phosphorus regeneration while concurrently limiting rotifer losses to less than 30% to minimize prey density effects.

Different preconditioning procedures were necessary to evaluate the effects of temperature and prey density of satiated and starved *Diacyclops*. All of the predators were held at a predetermined temperature for 18–24 h and at saturating *Synchaeta* densities ($500 \cdot L^{-1}$) for those experiments evaluating temperature. The experiments performed at 5 and 10°C required a 12-h duration and those at 15 and 20°C necessitated 6–8 h. The experiment assessing prey density effects on a sated predator used animals held for 18–24 h at 15°C and at a prey density of $500 \cdot L^{-1}$. The experiment was of 6 h duration. Starved *Diacyclops* were held without prey for 20–24 h at 15°C. They were then fed *Synchaeta* at the four prey densities for 4 h.

Diacyclops regeneration rates were estimated using a model developed and generously provided by Dr. Robert Dorazio (University of Michigan, Ann Arbor, MI, pers. comm.). This model assumes that the regeneration rates of *Synchaeta* (E_s) and *Diacyclops* (E_d) are constant, the densities of *Synchaeta* (N_s) in the control beakers and of *Diacyclops* (N_d) in the experimental beakers are constant, and that *Synchaeta* densities decrease in the experimental beakers at a constant rate equal to a clearance rate (F) of the predator. The phosphorus concentration in the controls (P_c) will change with time (t) according to

$$(1) \quad dP_c/dt = E_s N_s.$$

The solution to equation (1) is

$$(2) \quad P_c(t) = E_s N_s t + C.$$

Since $P_c(0) = 0$ and $C = 0$, the regeneration rate of *Synchaeta* (E_s) is

$$(3) \quad E_s = P_c(t')/t'N_s$$

where t' = the incubation time (hours) of any single experiment. Assume that

$$(4) \quad dN_s/dt = -FN_d N_s$$

whose solution is

$$(5) \quad N_s(t) = N_s(0)e^{-FN_d t}$$

where $N_s(0) = N_s$ at $t = 0$. If N_d is assumed constant, then

$$(6) \quad dP_e/dt = E_d N_d + E_s N_s.$$

N_s is a function of time in the experimental beakers. Substituting equation (5) into equation (6) gives

$$(7) \quad dP_e/dt = E_d N_d + E_s N_s e^{-FN_d t}.$$

Assuming that E_s is equal in the control and experimental beakers, equation (3) can be substituted into equation (7), giving

$$(8) \quad dP_e/dt = E_d N_d + (P_c(t')/t'N_{s,c})N_s(0)e^{-FN_d t}$$

where $N_{s,c}$ is the *Synchaeta* density in the control beaker. To estimate E_d, the regeneration of *Diacyclops*, the solution to equation (8) is

$$P_e(t) = \int E_d N_d dt + (P_c(t')/t'N_{s,c}) \int N_s(0)e^{-FN_d t}$$

$$(9) \quad P_e(t) = E_d N_d t - [P_c(t')N_s(0)/t'N_{s,c}FN_d]e^{-FN_d t} + C.$$

Since $P_e = 0$ at $t = 0$,

$$(10) \quad C = P_c(t')N_s(0)/t'N_{s,c}FN_d.$$

Substituting equation (10) into equation (9) gives

$$(11) \quad P_e(t) = E_d N_d t + [P_c(t')N_s(0)/t'N_{s,c}FN_d](1 - e^{-FN_d t}).$$

Finally, equation (11) is solved for E_d:

$$(12) \quad E_d = P_e(t') - [P_c(t')N_s(0)/t'FN_d N_{s,c}] \times (1 - e^{-FN_d t'})(t'N_d)^{-1}$$

where F, the clearance rate (litres per *Diacyclops* per hour), is

$$F = 1/t'N_d[\ln(N_s(0)/N_s(t'))].$$

Results

Diacyclops regeneration rates significantly increased in a linear fashion with temperature for SRP and TDP over the 5–20°C temperature range (Fig. 1). A more functional approach was to assume that regeneration was correlated with predation rate, which in turn was a function of temperature (Table 1). The linear correlation coefficient between regeneration and predation rates confirmed this relationship ($r = 0.97$, $P < 0.05$, Snedecor and Cochran 1972).

The first experiment relating prey density to phosphorus regeneration began with satiated individuals that had full guts and were lethargic. Some were even resting on the bottoms of the beakers. Regeneration rates increased in a curvilinear fashion to a maximum at the highest prey density offered, 500 *Synchaeta*$\cdot L^{-1}$ (Fig. 2). The two curves were fitted with second-order polynomials. Note that without prey present al-

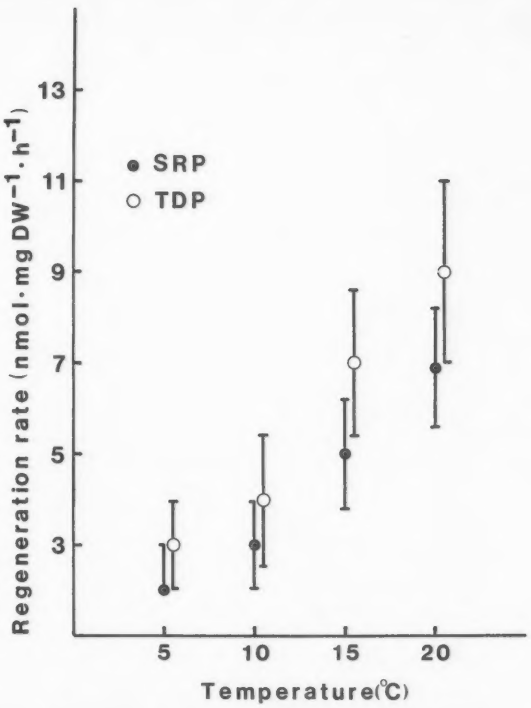


FIG. 1. Mean phosphorus regeneration rates (SE, $n = 3$) of *Diacyclops thomasi* versus temperature (°C) at a constant prey density of 500 *Synchaeta*·L^{-1}. Linear regression of SRP versus temperature, $Y = 0.3X - 0.1$, $R^2 = 0.98$, t-test for significance of regression $P < 0.01$, and for TDP versus temperature, $Y = 0.4X - 0.5$, $R^2 = 0.97$, t-test for significance of regression $P < 0.01$.

TABLE 1. Mean predation rates and phosphorus (SRP) regeneration rates (SE, $n = 3$) of *Diacyclops thomasi* at different temperatures and a constant *Synchaeta* prey density of 500·L^{-1}.

Temperature (°C)	Predation rate (prey consumed·h^{-1})	Regeneration rate (nmol P·mg dry wt^{-1}·h^{-1})
5	0.13 (0.05)	1.0 (1.0)
10	0.55 (0.13)	2.1 (1.5)
15	0.81 (0.02)	3.9 (1.6)
20	1.09 (0.10)	6.2 (2.0)

most all of the regenerated phosphorus was SRP. When prey were present, there was an increase in TDP most likely originating from either inefficient ingestion (bursting of *Synchaeta* during consumption) or from released fecal material which was not quantitatively measured. These rates were directly correlated with predation rates ($r = 0.95$, $P < 0.10$, Snedecor and Cochran 1972), which also increased with prey density (Table 2). At 500 *Synchaeta*·L^{-1}, fecal material was much more noticeable in the experimental beakers, but was not present as coherent pellets.

In the second experiment the cyclopoids had been starved for approximately 1 d. These predators, when introduced to the rotifer prey, were immediately very active and began searching for prey. Phosphorus regeneration rates increased curvilinearly to a maximum rate that was significantly greater than the maximum rates for sated *Diacyclops* (Student's t-test, $P < 0.05$, Snedecor and Cochran 1972). Second-order polynomials confirmed the nonlinear response (Fig. 3). A nearly perfect linear correlation ($r = 0.98$, $P < 0.01$, Snedecor and Cochran 1972) again existed between the regeneration and predation rates (Table 2).

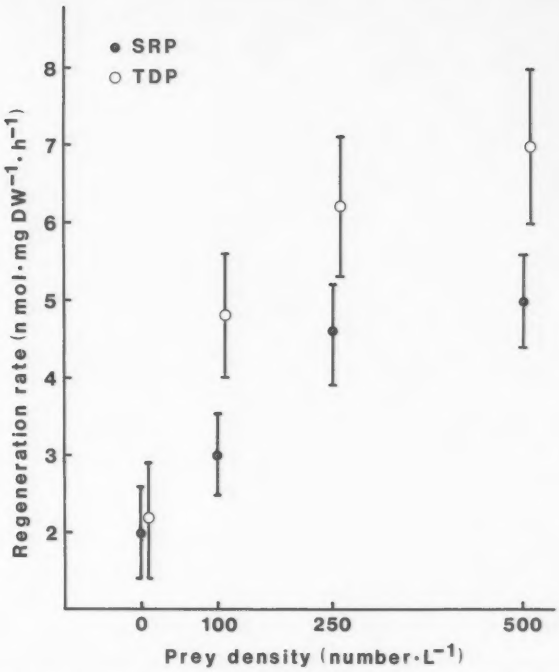


FIG. 2. Mean phosphorus regeneration rates (SE, $n = 3$) of satiated *Diacyclops thomasi* at three *Synchaeta* prey densities. Polynomial regression for SRP versus density, $Y = 0.014X - 0.00002X^2 + 0.8$, $R^2 = 0.99$, and for TDP versus density, $Y = 0.023X - 0.00003X^2 + 0.03$, $R^2 = 0.98$.

TABLE 2. Mean predation rates and phosphorus (SRP) regeneration rates (SE, $n = 3$) of satiated and starved *Diacyclops thomasi* at different *Synchaeta* prey densities at a constant temperature of 15°C.

Prey density (number·L^{-1})	Predation rate (prey consumed·h^{-1})	Regeneration rate (nmol P·mg dry wt^{-1}·h^{-1})
	Satiated Cyclops	
0	0.00 (0.00)	1.0 (0.60)
100	0.15 (0.04)	2.1 (0.55)
250	0.60 (0.24)	3.6 (0.63)
500	0.79 (0.18)	4.0 (0.64)
	Starved Cyclops	
0	0.00 (0.00)	0.8 (0.50)
100	0.56 (0.22)	2.3 (0.61)
250	1.79 (0.36)	5.6 (1.04)
500	2.54 (0.41)	7.1 (1.08)

Discussion

The phosphorus regeneration rates of *Diacyclops* are well within the range observed for herbivorous species in spite of the

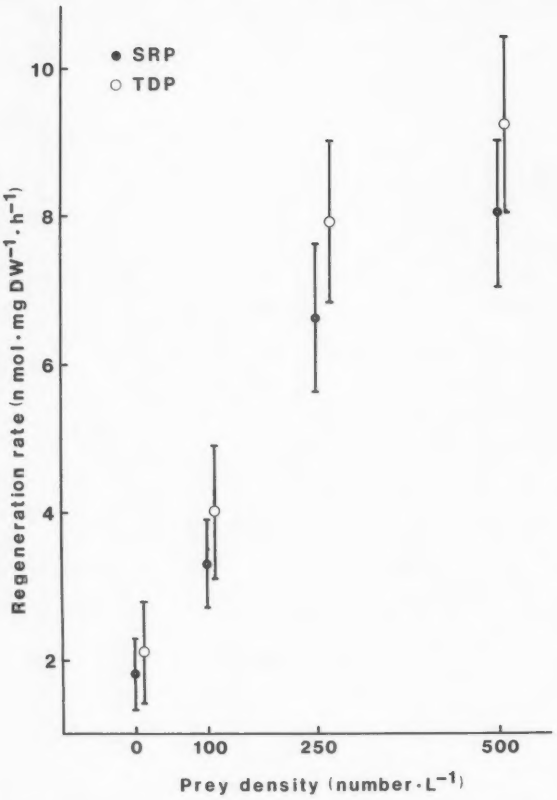


FIG. 3. Mean phosphorus regeneration rates (SE, $n = 3$) of starved *Diacyclops thomasi* at three *Synchaeta* prey densities. Polynomial regression for SRP versus density, $Y = 0.025X - 0.00003X^2 + 0.7$, $R^2 = 0.98$, and for TDP versus density, $Y = 0.03X - 0.00003X^2 + 1$, $R^2 = 0.98$.

variety of experimental methods, temperature differences, and nutritional preconditioning. Table 3 illustrates this range and is not meant to be comprehensive. My unpublished estimates for the rotifers *Asplanchna* and *Synchaeta* indicate substantially higher zooplankton regeneration rates because of their higher metabolic rates per unit biomass relative to crustacean zooplankton. When compared with the phosphorus regeneration rates from natural zooplankton assemblages in Lake Washington (Lehman 1980a) and Lake Huron (Korstad 1983), *Diacyclops* only approaches these rates when given an optimal prey at summertime epilimnetic temperatures.

The significant impact of temperature on the regeneration rates of *Diacyclops* concurred with previous investigations of marine and freshwater species for phosphorus excretion (Jawed 1969; Peters 1972; Peters and Rigler 1973; Taguchi 1976). More importantly, these results indicate the time of day and depths where nutrient regeneration will increase because of diel vertical migration. Regeneration rates are higher in the mixed layer of stratified lakes (Barlow and Bishop 1965; Ferrante 1976) and are also correlated with increased zooplankton feeding at night in these warmer strata (Hargrave and Geen 1968). In the Great Lakes, *Diacyclops* has a well-defined diel vertical migration pattern where, during the day, late copepodid stages and adults are found scattered throughout the thermocline region. At night they ascend and concentrate in the near surface waters (Wells 1960; Wilson and Roff 1973). This diel cycle exposes *Diacyclops* to a maximum temperature range of approximately 5–22°C. Regeneration rates would therefore increase during the evening hours in the mixed layer.

TABLE 3. Phosphorus regeneration rates (μmol P · mg dry $wt^{-1} \cdot h^{-1}$) of some representative zooplankton.

Species	Rate	Source
Diacyclops thomasi	0.1–0.8	This study
Asplanchna priodonta	0.5–4.0	J. A. Bowers (unpubl. data)
Synchaeta pectinata	0.4–7.4	J. A. Bowers (unpubl. data)
Daphnia pulex	0.5–0.7	Lehman 1980b
Daphnia magna	0.1	Rigler 1961
Thermocyclops hyalinus	1.5	Ganf and Blazka 1974
Acartia tonsa	0.1	Hargrave and Geen 1968
Acartia tonsa and *Acartia clausi*	0.5	Martin 1968
Natural assemblage	0.2–0.6	Lehman 1980a
Natural assemblage	0.6–1.2	Korstad 1983

Prey densities, their associated predation rates, and the consequent regeneration rates will also fluctuate owing to density variation imposed by zooplankton vertical migrations, seasonal succession, and the horizontal patchiness of *Diacyclops* prey species. Freshwater *Daphnia* (Peters 1972; Peters and Rigler 1973) and marine herbivore assemblages (Martin 1968) have phosphorus regeneration rates proportional to phytoplankton densities. In this study, *Diacyclops* regeneration rates increased nonlinearly with *Synchaeta* mortality rates and densities. Small changes in prey density result in amplified changes in phosphorus regeneration. This is particularly important to the migrating *Diacyclops* that feed on rotifers and copepod nauplii. For example, during thermal stratification in Lake Michigan, rotifer prey species are concentrated at several depths (Stemberger 1974). Copepod nauplii are found only in the epilimnion (Warren 1983). Thus, depth changes of only a few metres during the migration cycle place *Diacyclops* in significantly different prey environments. Predation rates and their resulting regeneration rates would respond to these changes.

Future studies should investigate invertebrate predator "selectivity" and how invertebrate zooplankton predators might influence the phosphorus regeneration rates of their prey populations. Similar to other zooplankton predators, *Diacyclops* has predation rates dependent on prey density, size, morphology, and swimming escape behavior (Stemberger 1982). These prey features quantitatively affect nutrient regeneration rates, while prey size and morphology qualitatively affect regenerative processes. In this study the small soft-bodied *Synchaeta* was ingested whole by the cyclopoid. Other rotifers, particularly loricate species, and larger crustacean prey with morphological defenses (Dodson 1974) must be manipulated and consumed in pieces. This inefficient ingestion will release unknown amounts of phosphorus, other than SRP, from prey parts into the surrounding waters.

Differential predatory behavior also shapes the species composition of prey populations (Kerfoot 1977). Cyclopoids, such as *Diacyclops*, suppress "preferred" rotifer and naupliar prey abundances (Stemberger and Evans 1984). These prey groups would then play a lesser role in zooplankton community regen-

eration even though their nutrient regeneration rates per unit biomass are high (Johannes 1964; J. A. Bowers, unpubl. data). This first study of an invertebrate predator indicates the direct role played by copepod predators in community phosphorus dynamics. Future research should evaluate indirect effects through predation on community zooplankton regeneration.

Acknowledgments

The Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, supported this research including travel and publication costs (No. NA-81-RAH-003). I thank Drs. Wayne Gardner, Stephen Tarapchek, and Donald Scavia for their continued support. Drs. Susan Kilham, Robert Dorazio, H. A. Vanderploeg, John Korstad, Ms. Joann Cavaletto, and Mr. Stephen Schneider provided many helpful suggestions to the manuscript. Discussions concerning zooplankton regeneration with Dr. John Lehman were greatly appreciated.

References

BALCER, M. D., N. L. KORDA, AND S. I. DODSON. 1984. Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species. The University of Wisconsin Press, Madison, WI. 174 p.

BARLOW, J. P., AND J. W. BISHOP. 1965. Phosphorus regeneration by zooplankton in Cayuga Lake. Limnol. Oceanogr. 10(Suppl.): R15–R25.

CARTER, J. C. H. 1969. Life cycles of *Limnocalanus macrurus* and *Senecella calanoides*, and seasonal abundance and vertical distribution of various planktonic copepods in Parry Sound, Georgian Bay. J. Fish. Res. Board Can. 26: 2543–2560.

DODSON, S. I. 1974. Adaptive change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721–729.

FERRANTE, J. G. 1976. The role of zooplankton in the intrabiocoenotic phosphorus cycle and factors affecting phosphorus excretion in a lake. Hydrobiologia 49: 203–214.

GANF, G. G., AND P. BLAZKA. 1974. Oxygen uptake, ammonia and phosphate excretion by zooplankton of a shallow equatorial lake (Lake George, Uganda). Limnol. Oceanogr. 19: 313–325.

GANNON, J. E. 1972. A contribution to the ecology of zooplankton crustacea of Lake Michigan and Green Bay. Ph.D. thesis, University of Wisconsin. Madison, WI. 205 p.

GUILLARD, R. R. L. 1975. Culture of phytoplankton for feeding marine invertebrates, p. 29–60. *In* W. L. Smith and M. H. Chanley [ed.] Culture of marine invertebrate animals. Plenum Publishing Corp., New York, NY.

HARGRAVE, B. T., AND G. H. GEEN. 1968. Phosphorus excretion by zooplankton. Limnol. Oceanogr. 13: 332–343.

HAWKINS, B. E., AND M. S. EVANS. 1979. Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. J. Great Lakes Res. 5: 256–263.

JAWED, M. 1969. Body nitrogen and nitrogen excretion in *Neomysis rayii* Murdock and *Euphausia pacifica* Hansen. Limnol. Oceanogr. 14: 748–754.

JOHANNES, R. E. 1964. Phosphorus excretion and body size in marine animals: microzooplankton and nutrient regeneration. Science (Wash., DC) 146: 923–924.

KERFOOT, C. W. 1977. Implications of copepod predation. Limnol. Oceanogr. 22: 316–325.

KORSTAD, J. 1983. Nutrient regeneration by zooplankton in southern Lake Huron. J. Great Lakes Res. 9: 374–388.

LEHMAN, J. T. 1980a. Nutrient recycling as an interface between algae and grazers in freshwater communities, p. 253–263. *In* W. C. Kerfoot [ed.] The ecology and evolution of zooplankton communities. New England Press, Hanover, NH.

1980b. Release and cycling of nutrients between planktonic algae and herbivores. Limnol. Oceanogr. 25: 620–632.

MARTIN, J. H. 1968. Phytoplankton relationships in Narragansett Bay. III. Seasonal changes in zooplankton excretion rates in relation to phytoplankton abundance. Limnol. Oceanogr. 13: 63–71.

MENZEL, D., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

PETERS, R. H. 1972. Phosphorus regeneration by zooplankton. Ph.D. thesis, University of Toronto, Toronto, Ont. 205 p.

PETERS, R. H., AND F. H. RIGLER. 1973. Phosphorus release by *Daphnia*. Limnol. Oceanogr. 18: 821–839.

RIGLER, F. H. 1961. The uptake and release of inorganic phosphate by *Daphnia magna* Straus. Limnol. Oceanogr. 6: 165–174.

SNEDECOR, G. W., AND W. G. COCHRAN. 1972. Statistical methods. Iowa State University Press, Ames, IA. 593 p.

STEMBERGER, R. S. 1974. Temporal and spatial distributions of planktonic rotifers in Milwaukee Harbor and adjacent Lake Michigan, p. 120–134. *In* Proc. 17th Conf. Great Lakes Res. International Association for Great Lakes Research, Toronto, Ont.

1982. Mechanisms controlling selection and rates of predation on rotifers in *Cyclops bicuspidatus thomasi*. Ph.D. thesis, University of Michigan, Ann Arbor, MI. 106 p.

STEMBERGER, R. S., AND M. EVANS. 1984. Rotifer seasonal succession and copepod predation in Lake Michigan. J. Great Lakes Res. 10: 417–428.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. 2nd. ed. Bull. Fish. Res. Board Can. 167: 310 p.

TAGUCHI, S. 1976. Microzooplankton and seston in Akkeshi Bay, Japan. Hydrobiologia 50: 195–204.

TAKAHASHI, M., AND T. IKEDA. 1975. Excretion of ammonia and inogranic phosphorus by *Euphausia pacifica* and *Metridia pacifica* at different concentrations of phytoplankton. J. Fish. Res. Board Can. 32: 2189–2195.

TORKE, B. G. 1975. The population dynamics and life histories of crustacean zooplankton at a deep-water station in Lake Michigan. Ph.D. thesis, University of Wisconsin, Madison, WI. 236 p.

WARREN, G. J. 1983. Predation by *Limnocalanus* as a source of winter naupliar mortality in Lake Michigan. J. Great Lakes Res. 9: 389–395.

WATSON, N. H. F., AND G. F. CARPENTER. 1974. Seasonal abundance of crustacean zooplankton and net plankton biomass of Lakes Huron, Erie, and Ontario. J. Fish. Res. Board Can. 31: 309–317.

WELLS, L. 1960. Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 60: 343–369.

WILSON, J. B., AND J. C. ROFF. 1973. Seasonal vertical distributions and diurnal migration patterns of Lake Ontario crustacean zooplankton, p. 190–203. *In* Proc. 16th Conf. Great Lakes Res. International Association for Great Lakes Research, Toronto, Ont.

A Radiotracer Study of Phosphorus Cycling in a Eutrophic Canadian Shield Lake, Lake 227, Northwestern Ontario[1]

S. N. Levine,[2] M. P. Stainton, and D. W. Schindler

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6

Levine, S. N., M. P. Stainton, and D. W. Schindler. 1986. A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227, northwestern Ontario. Can. J. Fish. Aquat. Sci. 43: 366–378.

Phosphoric acid labelled with ^{32}P was added to the epilimnion of experimentally eutrophied Lake 227, northwestern Ontario, in August 1978 to trace the lake's phosphorus cycle during late stratification and fall overturn. Radiophosphate was incorporated into bacteria and microphytoplankton (<10 μm in diameter) within minutes of introduction. Thereafter, the bulk of ^{32}P exchange was between the microplankton, which typically held >90% of ^{32}P, dissolved phosphate, and a mobile subcompartment of "dissolved organic" phosphorus. Phytoplankton >10 μm in diameter and zooplankton acquired ^{32}P label very slowly and contained <5% of the radiotracer. In addition, about half of dissolved organic phosphorus failed to acquire a ^{32}P label over 17 d of incubation, indicating that this phosphorus may be functionally inert, at least at the time scale of biological phosphorus exchange. Movement of ^{32}P to the littoral zone of Lake 227 was much slower than in lakes with well-developed macrophyte communities, but losses to deep sediments were similar, about 2% of ^{32}P per day. Particles settled through the hypolimnion at a modal velocity of 28 $cm \cdot d^{-1}$, losing 10% or less of their ^{32}P during descent. Most of the released phosphorus was reincorporated into particles and sedimented. Less than 1% of the ^{32}P that entered the hypolimnion in particles between August and October remained in the hypolimnion in late October. ^{32}P release from Lake 227's hypolimnetic sediments during late summer and fall of 1978 was <5% of the ^{32}P that sedimented.

En août 1978, on a ajouté à l'épilimnion du lac 227, rendu eutrophe expérimentalement et situé dans le nord-ouest de l'Ontario, de l'acide phosphorique marqué au ^{32}P, afin de suivre le cycle du phosphore dans le lac à la fin de la stratification et pendant la période de circulation d'automne. Le phosphate radioactif s'est intégré aux bactéries et au phytoplancton microscopique (diamètre <10 μm) en l'espace de quelques minutes après l'introduction du produit. Par la suite, la plus grande partie de l'échange de ^{32}P s'est faite entre le microplancton, qui, typiquement, contenait plus de 90 % du ^{32}P, le phosphate dissous et une partie mobile de phosphore « organique dissous ». Le phytoplancton d'un diamètre >10 μm et le zooplancton ont été marqués très lentement au ^{32}P et contenaient moins de 5 % du traceur radioactif. De plus, environ la moitié du phosphore organique dissous n'a pas été marqué au ^{32}P après 17 j d'incubation, ce qui indique que ce phosphore pourrait être inerte du point de vue fonctionnel, du moins à l'échelle temporelle du processus biologique d'échange de phosphore. Le déplacement de ^{32}P vers la partie littorale du lac 227 s'est fait beaucoup plus lentement que dans les lacs où l'on trouve des communautés de macrophytes bien développées, mais les pertes vers les sédiments profonds ont été semblables, soit environ 2 % de ^{32}P par jour. Les particules ont traversé l'hypolimnion à une vitesse modale de 28 $cm \cdot j^{-1}$, perdant 10 % au moins de leur ^{32}P au cours de leur descente. La plus grande partie du phosphore libéré s'est réintégrée aux particules et s'est sédimentée. Moins de 1 % du ^{32}P qui a pénétré dans l'hypolimnion associé aux particules entre août et octobre est demeuré dans l'hypolimnion à la fin d'octobre. La libération de ^{32}P à partir des sédiments de l'hypolimnion du lac 227 à la fin de l'été et à l'automne de 1978 représentait moins de 5 % du ^{32}P qui s'est sédimenté.

Received December 17, 1984
Accepted July 29, 1985
(J8047)

Reçu le 17 décembre 1984
Accepté le 29 juillet 1985

Addition of radiophosphorus as PO_4 to whole lakes is necessary to characterize phosphorus cycling at an ecosystem level (Schindler 1985; Schindler et al. 1975). Only by adding a tracer to one region of a lake and monitoring its movement into other regions can one measure gross phosphorus flux between lake regions. A whole-lake experiment also permits measurements of phosphorus flux among species of particulate and dissolved phosphorus under totally natural conditions. Several whole-lake radiophosphorus studies have been undertaken since radiotracer techniques were introduced in the late 1940's (Hutchinson and Bowen 1947, 1950; Coffin et al. 1949; Hayes et al. 1952; Rigler 1956; Chamberlain 1968). Although illuminating, these experiments had shortcomings. Measurements of phosphorus flux between lake regions were imprecise because there were major losses of radioisotope to unmonitored regions of the lake, so that all of the added ^{32}P could not be accounted for (Rigler 1973), and small additions of radioactivity limited the ability of investigators to quantify fluxes among phosphorus compart-

[1] Contribution No. ERC-088 of the Ecosystems Research Center, Cornell University, Ithaca, NY.

[2] Present address: Ecosystems Research Center, Corson Hall, Cornell University, Ithaca, NY 14853, USA

ments. Early analyses of whole-lake ^{32}P dynamics included no more than two phosphorus compartments (dissolved and suspended particulate phosphorus) (Hutchinson and Bowen 1947, 1950; Rigler 1956) and sometimes only one compartment (dissolved phosphorus) (Coffin et al. 1949; Hayes et al. 1952). By using more radioactivity and more efficient radioassay methods, Chamberlain (1968) increased the number of phosphorus pools examined to four: phosphorus within the size ranges <0.1, 0.1–0.45, 0.45–70, and >70 μm.

During the summer of 1978, we added 370 Bq (10.0 Ci) of ^{32}P-labelled phosphate to the epilimnion of eutrophic Lake 227 in northwestern Ontario. This amount was sufficient to allow us to trace the movement of phosphorus through the lake for several weeks, despite the short half life of ^{32}P, and to examine eight epilimnetic phosphorus compartments. The Lake 227 experiment had the additional advantage of a precisely known phosphorus "loading." Over 90% of the lake's phosphorus enters as phosphate fertilizer, added as equal weekly doses during the ice-free season (Cruikshank 1984). Fertilization had been carried out for 10 yr at the time of this experiment, and an analysis of nutrient budgets indicated that the lake was in equilibrium with its artificial nutrient loading (D. W. Schindler, R. H. Hesslein, and M. A. Turner, unpubl. data). The experiment was initiated in late summer, when steady-state conditions between phosphorus input and the flux of phosphorus among fractions in the lake should exist, if they occur at all (Rigler 1973). Careful monitoring of the radioactivity in the lake's outflow, sediments, and water column strata permitted construction of the first balanced budget for ^{32}P fate and transport in a whole lake.

Lake Description

Lake 227 is a small (area = 5.0 ha), round, headwater lake in the Experimental Lakes Area (ELA) of northwestern Ontario (49° 41′N, 93°41′W). The lake has a mean depth of 4.4 m, a maximum depth of 10 m, and an average water renewal time of 2.8 yr (measured between 1970 and 1977, Newbury and Beaty 1980). Profundal sediments and about half of the littoral sediments are flocculent and highly organic (organic carbon = 23% of dry weight, Brunskill et al. 1971), while the remaining littoral sediments consist largely of silt, stones, and organic debris. Both submerged and emergent macrophytes are very rare, except for sedges of mosses in a small bog along the eastern shore (Brunskill and Schindler 1971).

In its natural condition, Lake 227 was oligotrophic, with chlorophyll concentrations of <2 $\mu g \cdot L^{-1}$ and Secchi depths >4 m (Schindler 1971; Schindler et al. 1971). Since 1969, however, the lake has been fertilized on a weekly basis during the summer with sodium nitrate (315 mg $N \cdot m^{-2} \cdot wk^{-1}$ from 1969 to 1974 and 113 mg $N \cdot m^{-2} \cdot wk^{-1}$ after 1975) and either disodium hydrogen phosphate (20 mg $P \cdot m^{-2} \cdot wk^{-1}$ in 1969) or phosphoric acid (25 mg $P \cdot m^{-2} \cdot wk^{-1}$ from 1970 to 1974 and 23 mg $P \cdot m^{-2} \cdot wk^{-1}$ after 1975). Typically, 20 or 21 weekly additions are made each year. Each weekly addition from 1975 on has consisted of dissolving the weekly dose of nutrients in 200 L of lake water and allowing this to drip from a hose connected to a tap on the bottom of a plastic barrel into the epilimnion of the lake. The flow rate is adjusted so that 4–6 d are required for the barrel to empty each week. Consequently, Lake 227 has the biology and chemistry of a eutrophic lake (Schindler 1975). The bottom waters of the lake are usually anaerobic for 10 or more months each year, since spring overturn is rarely complete below 7 m. The deepest part of the lake (9–10 m) has not mixed during either spring or fall overturn since 1974 or 1975 (D. W. Schindler, R. H. Hesslein, and M. A. Turner, unpubl. data).

On the day of radiophosphorus addition (11 August 1978), the epilimnion of Lake 227 was 2 m deep, the hypolimnion was anoxic from 5 m down, the outflow was dry, and the sky was cloudless. The weekly fertilization had begun 3 d before, so that the lake received a small amount of fertilizer during radiotracer addition. The phytoplankton community was dominated by small green algae (>60% of total biomass), while blue-green algae were second in abundance (Findlay 1981). *Oocystis submarina* var. *lacustris* alone accounted for more than one third of the phytoplankton biomass. Roughly the same phytoplankton community was maintained through mid-September. Thereafter, blue-green algae (chiefly *Aphanizomenon gracile*, which fixes nitrogen) increased in abundance, so that, during October, the green algal biomass and blue-green algal biomass were roughly equal. The zooplankton community at radioisotope addition consisted largely of cyclopoid and calanoid nauplii and copepodites, with *Diaphanosoma brachyurum* being the only abundant adult crustacean (Chang et al. 1980). Between mid-August and mid-September, the number of adult Crustacea was relatively constant, while the abundance of juveniles first dwindled and then increased to a second peak. After mid-September, the abundance of all life stages of Crustacea decreased. Although rare in early August, rotifers were very abundant in the epilimnion during late August and September (1000–6500 individuals $\cdot L^{-1}$) (Chang et al. 1980). In October, rotifer numbers diminished, but the zooplankton community was still rotifer-dominated.

Materials and Methods

Short-Term Radiophosphorus Uptake Experiments

Because the phosphorus uptake by algae and bacteria in ELA lakes typically is much faster than the time required for whole-lake radiophosphorus addition and sampling (Levine and Schindler 1980), the initial flux of $^{32}PO_4$ into seston was measured in vitro. On 11 August 1978, a vertically integrated sample was collected from the epilimnion minutes before the addition of radiophosphorus to the lake. Phosphoric acid labelled with ^{32}P (purchased from New England Nuclear) was added to beakers containing 200 mL of this water and the rate of incorporation of label into particles was measured (Levine 1975). Nuclepore filters with pore sizes of 0.2 μm were used to separate particulate and "dissolved" ^{32}P (the "dissolved" fraction included colloids and some minute particles), and 1-μm filters were used to estimate the proportion of the ^{32}P spike taken up by phytoplankton (excepting the picophytoplankton). The difference between the ^{32}P retained by 1-μm filters and that retained by 0.2-μm filters was an estimate of radioisotope incorporation into bacteria and picophytoplankton. During our experiment, microscopic examination revealed that large bacteria (>0.5 μm in diameter) were rare in Lake 227 (D. Findlay, Freshwater Institute, Winnipeg, Man., pers. comm.).

The reciprocal of the initial slope of the exponential regression of percent total ^{32}P activity in solution (i.e. in 0.2-μm filtrate) versus time yielded an estimate of the turnover time (T) of the epilimnetic phosphate pool (Riggs 1963):

$$T = 1/K \text{ and } K = (\ln 100 - \ln Y)/\text{time}$$

where Y is the percent ^{32}P in solution.

Spike Procedures

The radioisotope (370 Bq (10.0 Ci) of $H_3{}^{32}PO_4$)) and 28 L of distilled water were mixed in a polyethylene tub mounted in a canoe. The solution was dispersed over the surface of Lake 227 by towing the canoe back and forth across the lake surface with an outboard-powered boat while the solution was pumped from the tub through tygon tubing to eight syringe needles taped to a 4-m-long rod fastened across the back of the canoe. The solution sprayed onto the lake surface from a height of 0.5 m. This procedure took place at midday (roughly 11:00–13:30 CDT) while solar insolation was maximal. Earlier whole-lake mixing experiments in Lake 227 with tritium as a tracer had shown that a horizontally uniform distribution of a nonreactive, dissolved radiotracer could be expected within a few hours of tracer addition (Quay 1977). Horizontal mixing of ^{32}P, a tracer carried primarily in particles, may have required more time: some of the metal radiotracers that were added to ELA Lake 224 and subsequently incorporated into particles were patchily distributed for 1–2 d (Hesslein et al. 1980). However, the area of Lake 224 is five times that of Lake 227.

Size Fractionation of Epilimnetic Phosphorus

Collection of the first sample from the epilimnion of Lake 227 began 45 min after the end of the addition of radioisotope to the lake. To ensure vertically integrated samples, water was pumped up through weighted tygon tubing that was repeatedly lowered and raised between the surface and the bottom of the epilimnion (2 m). Because the horizontal distribution of radioisotope was expected to be patchy for several hours after the spike, this procedure was repeated at 10 randomly selected sites and the samples pooled. A 15-L composite sample was brought to a floating laboratory on Lake 227, where 1 L was passed sequentially through Nytex nylon filters that were 47 mm in diameter with nominal pore sizes of 200, 50 and 10 μm. Fifty millilitres of the 10-μm filtrate was then filtered through a Nuclepore membrane with a pore size of 1 μm and 25 mL of the 1-μm filtrate through a membrane with a pore size of 0.2 μm. After each filtration, the retained material (either particles washed from nylon netting or particles plus Nuclepore membranes) and 20 mL of filtrate were collected in scintillation vials for subsequent radiochemical and chemical analysis. All filtrations were performed in triplicate. Three to six 20-mL samples of whole water also were saved for radiochemical and chemical analysis.

The first fractionation of phosphorus forms by size took place 20 min after sampling began and about 2 h after the midpoint of the whole-lake spike. The procedure was repeated, usually between 13:00 and 15:00, on days 1–6, 10, 12, 14, 17, 32, 48, and 53. After the first day of the experiment, water collection was restricted to one station at the lake's deepest point. On days 42, 55, and 72, 1 L of 0.2-μm filtrate was passed sequentially through Amicon filters that retain molecules with nominal molecular weights of 100 000 and 1000 and the radioactivities of the fractions were determined. The phosphorus concentrations in these samples were too low for accurate measurement.

On days 105 and 150, samples were collected from 1 m below the ice. Because radioactivity was very low, the water was not filtered but used simply to determine the specific activity of total phosphorus. Samples were rotoevaporated from 1 L on day 105 and 7 L on day 150 to 20 mL before radioactivity and phosphorus content were measured.

On eight occasions during the first 2 wk of experimentation and on day 41, fathead minnow (*Pimephales promelas*) were collected from along the shores of Lake 227 with a dip net. The fish were dried and ashed and their radioactivities and phosphorus contents determined.

Vertical Profiles and Outflow

To ensure an accurate mass balance, the rate of descent of phosphorus through the water column was monitored. Samples were collected from discrete depths on days 1–8, 10, 12, 14, 17, 20, 23, 25, 32, 39, 48, 53, 68, 81, and 105. A 3-m-long close-interval syringe sampler was lowered in an overlapping series of hauls to just below the thermocline. Before day 20, the sampler used, which collected 10-mL samples, was pneumatically controlled and similar to the one described by Heaney (1974). After day 20, when diminished ^{32}P activity required larger samples for analysis, a spring-loaded sampler with 50-mL syringes (Quay 1977) was used.

Using the above devices, samples were taken at 50-cm intervals in the upper epilimnion and at 10-cm intervals in the lower epilimnion, the thermocline, and the upper hypolimnion. The lower hypolimnion was sampled at 1-m intervals with a peristaltic pump and tygon tubing. Five to 7 mL from each 10-mL syringe or 20 mL from each 50-mL syringe was placed in plastic scintillation vials for radiochemical analysis. For the final vertical profile (day 105), a peristaltic pump and tygon tubing were used to obtain 1-L samples at 2-m intervals.

Collection of water for vertical profiles was followed by the collection of 500 mL of water from the lake's outflow, if it was flowing. This sample was taken at the v-notch of a weir about 50 m downstream from the outlet. We measured both the radioactivity and total phosphorus concentration in the sample. Because flow through the weir was recorded continuously with a level recorder (Newbury and Beaty 1980), ^{32}P loss through the outflow was calculated as the product of radioactivity and flow.

Sediment Traps and Cores

Sediment traps, 50 cm in length and 22 cm in diameter at the mouth, were constructed from polyethylene bags in the manner described by Hesslein et al. (1980). The traps were set 1 m above the sediments in 3, 6, and 9 m of water. After 1–2 wk, the traps were closed by pulling nylon lines that formed nooses around the tops of the bags and then hauled to the surface. The traps were emptied in the laboratory into 2-L acrylic funnels that were closed at the bottom with rubber tubing and clamps. After the disturbed sediments resettled, they were drained through the tubing into glass scintillation vials and analyzed for both ^{32}P activity and total phosphorus.

On October 11 (day 61), when enough of the ^{32}P in Lake 227 had radiodecayed to ensure human safety, 13 sediment cores were collected along a transect between the bog and the center buoy (see the map in Brunskill and Schindler 1971). Acrylic tubes (5 cm in diameter, 20 cm in length) were pressed by a SCUBA diver into the sediments and the ends were sealed with rubber bungs. Care was taken to include an undisturbed sediment–water interface in each core.

In the laboratory, all but the bottom 2 cm of water overlying the sediments in the cores was drawn into a syringe through tygon tubing and discarded. The residual water and about 5 cm

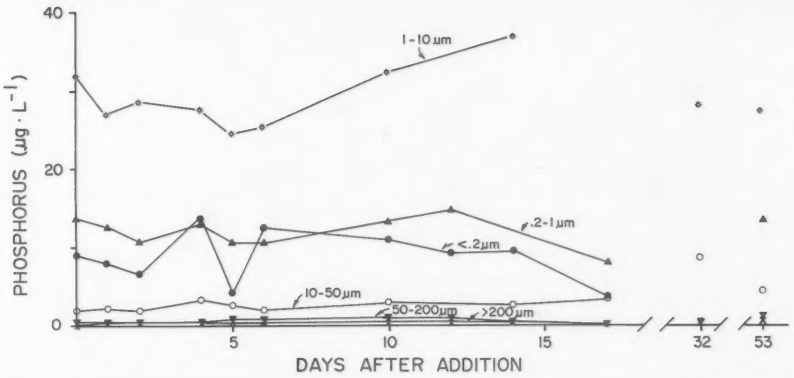


FIG. 1. Phosphorus concentrations in different size fractions in the epilimnion of Lake 227 during the 53 d that followed ^{32}P addition to the lake surface.

of sediment were then sucked into the syringe and emptied into glass scintillation vials for ashing (500°C) and radiochemical analysis.

Counting Procedures and Chemical Analysis

Radiophosphorus activity was measured by Cerenkov counting (Brown 1971), using a Picker Nuclear Liquimat 220 or a Nuclear Chicago Unilux II scintillation counter. Blanks and standards were formed using sediments and water collected before the spike. The measured activities were corrected for radioactive decay. Particulate and total phosphorus were measured by igniting dried filters, the residue of evaporated whole-water samples or dried sediment samples at 500°C, acidifying the ash and analyzing for soluble reactive phosphorus (Stainton et al. 1977). Dissolved phosphorus was measured by exposing acidified filtrate to ultraviolet radiation for 4 h and analyzing for soluble reactive phosphorus (SRP) (Stainton et al. 1977).

Results

Radiophosphorus Exchange Among Phosphorus Fractions in the Epilimnion of Lake 227

During the 53-d interval when we examined ^{32}P exchange among phosphorus fractions in the epilimnion, the phosphorus contents of the studied fractions fluctuated within reasonably narrow ranges (Fig. 1), suggesting that the flux of phosphorus among pools was at a quasi-steady state. However, exceptionally high amount of phosphorus were measured for the 1- to 10-μm fraction on day 14 and for the 10- to 50-μm fraction on day 32.

Short-term in vitro measurements of $^{32}PO_4$ disappearance from lake water indicated that on the morning of radiophosphorus addition to Lake 227, the phosphate pool in the epilimnion was turning over every 3 min. Ten minutes after $^{32}PO_4$ was added, 70% of the radioisotope was in particles retained by membranes with 1-μm pores. An additional 24% of the ^{32}P passed through the 1-μm filters, but was retained by membranes with 0.2-μm pores. At this time, the specific activities of the 0.2- to 1-μm and >1-μm phosphorus fractions were similar (10 370 vs. 10 260 cpm·L^{-1}), while the specific activity of dissolved phosphorus was much lower (2050 cpm·L^{-1}). Particles >1 μm in diameter incorporated more radiotracer than 0.2- to 1-μm-diameter particles because they were very abundant and contained a greater portion of the phosphorus pool. All but a tiny portion of the radiotracer (<6%) therefore entered particles before we began whole-lake sampling.

Two hours after the addition of isotope, ^{32}P in the lake was similarly partitioned between particles and solution (Fig. 2). Subdivision of the >1-μm particulate phosphorus pool showed that the pool's smallest particles were responsible for most ^{32}P uptake by the pool: <5% of sestonic ^{32}P was in particles >10 μm in diameter and the specific activities of particles >10 μm in diameter were 1−2 orders of magnitude less than the specific activities of smaller particles (see Fig. 4). However, particles >10 μm in diameter were not abundant in Lake 227.

A similar relative distribution of radioisotope among suspended phosphorus pools was maintained during the next 52 d, except that the proportion of ^{32}P in the 10- to 50-μm compartment increased slightly between days 14 and 32. The increase in the ^{32}P contents of intermediate-sized particles occurred at the expense of the ^{32}P stores in both smaller particles and the "dissolved" phase.

New, unlabelled phosphorus entered the epilimnion of Lake 227 from weekly fertilization and periodic precipitation and runoff throughout the experiment, causing the specific activity of total phosphorus to decrease with time (Fig. 3). Therefore, to compare the specific activities of individual phosphorus compartments, we normalized all specific activities to the specific activity of total phosphorus. We found that, despite the fairly stable distribution of ^{32}P among phosphorus compartments, full isotopic equilibrium (equal $^{32}P/^{31}P$ ratios in all phosphorus compartments, the equilibrium ratio being total ^{32}P/total ^{31}P) was not attained for at least 17 d after ^{32}P addition and may have never occurred. During the first 2 d of the experiment (but after the first few minutes of incubation), particles 0.2−10 μm in diameter had specific activities that were at least double the specific activity of the 0.2-μm filtrate, and six or more times the specific activities of particles >10 μm in diameter (Fig. 4). Between days 2 and 17, the specific activities of particles 0.2−10 μm in diameter decreased relative to the specific activity of total phosphorus, while the specific activities of particles >10 μm rose toward, but did not reach, the equilibrium value. After day 17, our data analysis was incomplete because low phosphorus concentrations in some compartments (Fig. 1) prohibited the calculation of many specific activities. However, extrapolation of the plots of specific

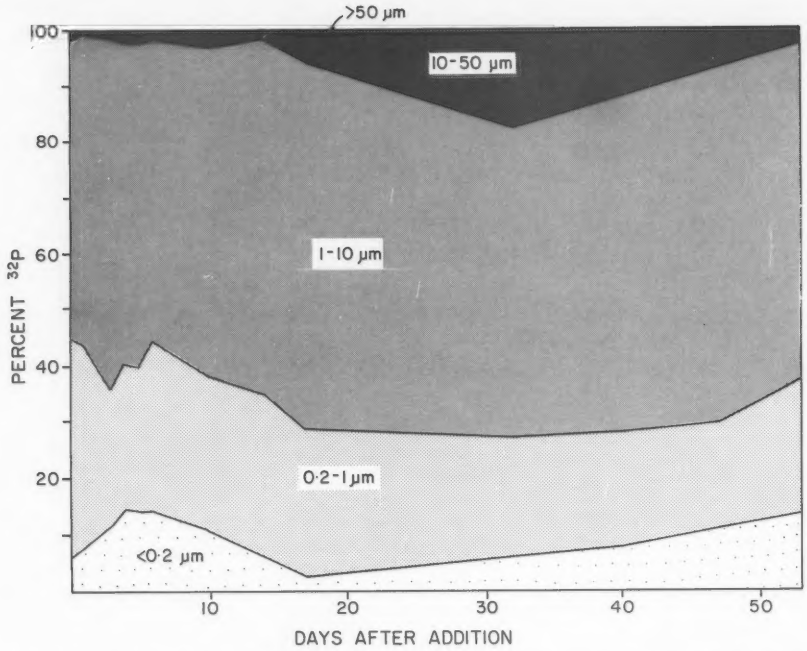


FIG. 2. Relative distribution of ^{32}P among size fractions in the epilimnion of Lake 227 during the 53 d that followed ^{32}P addition to the lake surface.

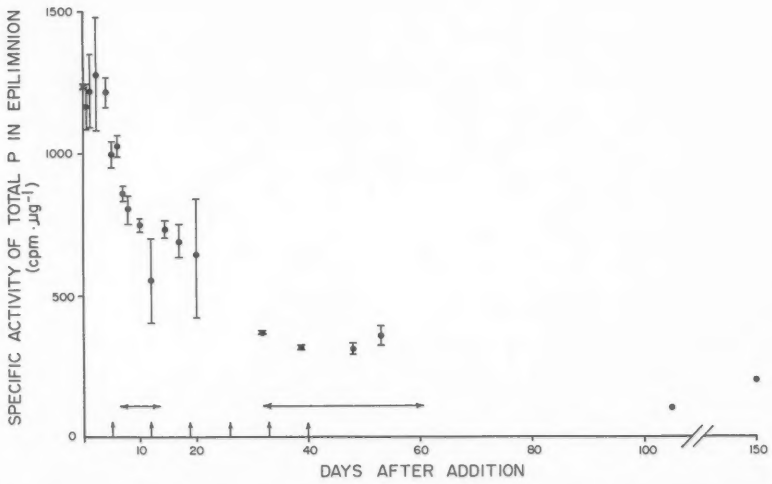


FIG. 3. Measured specific activity of total phosphorus (with 90% confidence limits) in the epilimnion versus time. Vertical arrows identify the dates when phosphorus fertilizer was added to the lake, and horizontal arrows identify periods of thermocline deepening. The "x" on the *y*-axis is the expected initial specific activity calculated from the assayed ^{32}P addition and total phosphorus.

activity versus time for days 0–17 suggests that full labelling of particles 10–200 μm in diameter required close to 1 mo and complete labelling of particles >200 μm even more time. Actual measurements of specific activity showed that the 10- to 50-μm-diameter particles were near isotopic equilibrium on day 32.

For the first 2 wk of experimentation, minnows were labelled at roughly the same rate as particles >200 μm. Later, the rate of labelling must have increased slightly, because the minnows collected on day 41 had specific activities greater than equilibrium specific activity.

The labelling of the "dissolved" phosphorus (DP) compartment (the 0.2-μm filtrate) occurred in a manner that suggested the existence of two or more subcompartments, the subcom-

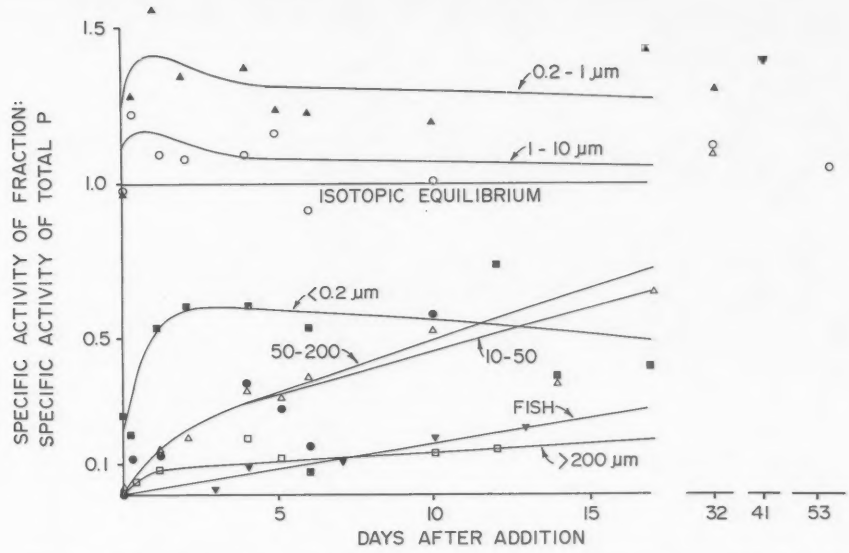


FIG. 4. Specific activities of the phosphorus size fractions in the epilimnion of Lake 227 after ^{32}P addition, relative to the specific activity of total phosphorus (1.0). The lines were drawn by eye.

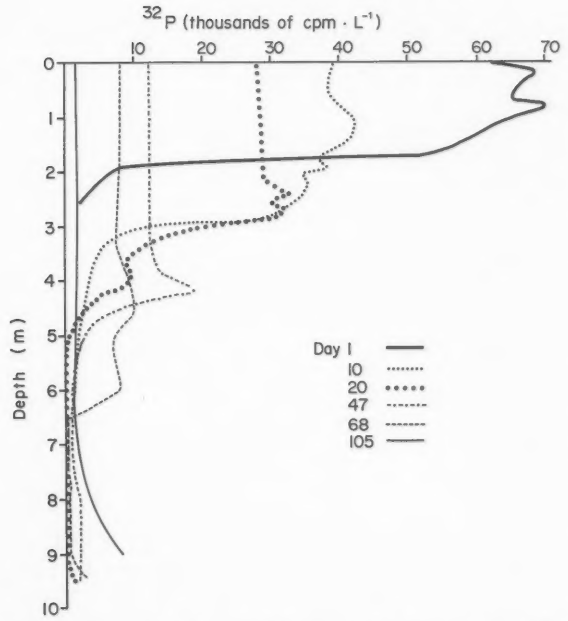


FIG. 5. Examples of the vertical profiles for ^{32}P activity in Lake 227 during the first 105 d following ^{32}P addition to the epilimnion. The lines were drawn through the data points.

partments being either different phosphorus compounds or different phosphorus bonds on similar compounds. The specific activity of DP was about half the equilibrium specific activity within 2 d of ^{32}P addition, but thereafter (from day 3 to 17) the specific activity of the compartment seems to have declined relative to equilibrium specific activity. The rate of decline was similar to the rate of decrease in small-particle specific activity relative to equilibrium specific activity (as shown by the similarity of slopes in Fig. 4). This observation suggests that the 0.2- to 1-µm, 1- to 10-µm, and <0.2-µm phosphorus compartments exchanged at least some phosphorus readily and, therefore, developed a quasi-steady state distribution of radioisotope within 2 or 3 d of radioisotope addition. The heights of the plots of specific activity versus time for the three compartments probably differed because each phosphorus compartment contained variable amounts of both "mobile" and inert phosphorus.

The molecular weights of the exchanging and nonexchanging pools in DP could not be accurately determined because both the radioactivity and the phosphorus content of the Amicon fractions were too low to calculate specific activities with reasonable precision. However, Amicon fractionation showed that between one half and two thirds (47, 59, and 69%; $n = 1$) of dissolved ^{32}P (the <0.2-µm phosphorus compartment) was in high molecular weight colloids or minute particles (molecular weight >100 000). The other one third to one half of dissolved ^{32}P was in compounds with molecular weights between 1000 and 100 000. The radioactivity of the <1000 molecular weight fraction, which included $^{32}PO_4$, was not distinguishable from background radioactivity. It is possible that $^{32}PO_4$ adsorption onto Amicon filters exaggerated the smallness of the <1000 molecular weight compartment. We did not measure $^{32}PO_4$ adsorption during our experiments. Recently, we filtered solutions of phosphate (100 µg $P \cdot L^{-1}$) through Amicon filters and recovered 100% of the phosphorus. However, adsorption may be more significant at low phosphate concentrations.

Radiophosphorus Exchange Among Lake Regions

While Lake 227 was thermally stratified, ^{32}P activity in the epilimnion exceeded that in the hypolimnion by two or more orders of magnitude (Fig. 5). Only when the thermocline deepened and Lake 227 mixed did substantial amounts of ^{32}P reach depths below 4 m (beginning around day 40). The vertical

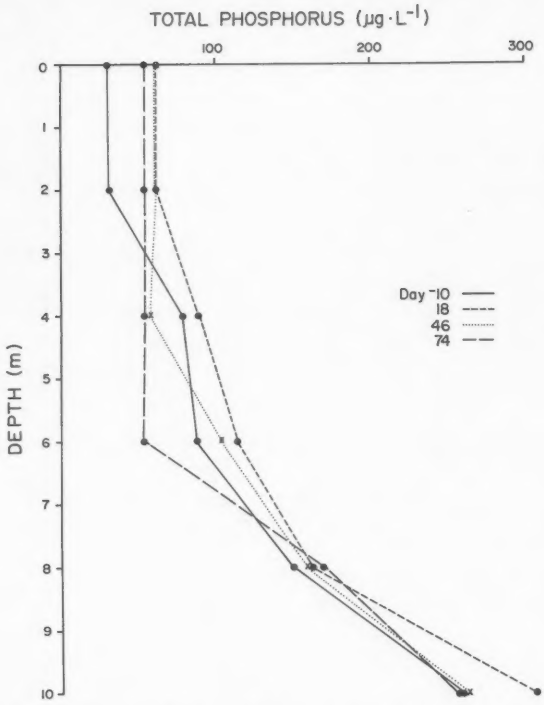


FIG. 6. Examples of the vertical profiles for total phosphorus in Lake 227 during the radiotracer experiment.

profiles for ^{32}P contrasted sharply with the profiles for nonradioactive phosphorus (Fig. 6), which showed greater concentrations at depth due to the funneling of descending particles into less water and the accumulation of dissolved phosphorus in deep water over a year or more.

Radiophosphorus, however, did not remain wholly in the epilimnion and thermocline. Vertical profiles showed a steady decline of ^{32}P activity in the epilimnion with time (Fig. 5), and mass balance calculations indicated that one half of the radioisotope disappeared from the water column before day 40 (Fig. 7). By day 105, less than 10% of the added ^{32}P was still in the water column.

As in other whole-lake radiotracer experiments, carried out in lakes that were chosen to have reasonably slow hydraulic flushing, very little (3%) of the ^{32}P that was added to Lake 227 left through the outflow (Fig. 7). Most of the radioisotope sedimented. From the sediment cores, we estimated that 3.67×10^{12} cpm of ^{32}P lay in surface sediments on day 61 (Table 1). Mass balance calculations of the cumulative nonoutflow ^{32}P loss up to day 61 (3.84×10^{12} cpm) agreed with this value to within 5%.

While radiotracer experiments in lakes with borders of macrophytes (Rigler 1973) consistently have shown ^{32}P losses from the water column that are diphasic or multiphasic (i.e. the losses must be described as multiple exponential functions rather than single exponential functions), the exponential regression of total ^{32}P activity in Lake 227 over time was strictly monophasic (Fig. 8). The correlation coefficient for the regression was highly significant, and the initial ^{32}P content predicted by the *y*-intercept of the regression (317 Bq) was close to the assayed addition (370 Bq). Monophasic ^{32}P loss indicates one-way phosphorus exchange between two compartments, or, less likely, one-way losses from one compartment to two or more compartments, provided the losses are nearly equal in magnitude. In this case, we interpret the results as a one-way transfer of ^{32}P from the water column to the sediments.

Phosphorus Sedimentation in Lake 227

Because ^{32}P losses via the outflow were negligible, the slope of the exponential regression of total ^{32}P activity in the water column of Lake 227 versus time, $2.1\% \cdot d^{-1}$, approximated the sedimentation rate of phosphorus from the lake. This value should be corrected to account for the fact that only particulate ^{32}P sedimented. The particle-specific phosphorus sedimentation rate was $2.2\% \cdot d^{-1}$. The attrition of ^{32}P from the epilimnion alone was 1.9% of particulate $P \cdot d^{-1}$. These values are similar to those calculated from mass balance budgets early in the Lake 227 experiment (Schindler et al. 1973). Overall, the residence time for phosphorus in the epilimnion of Lake 227 was 53 d.

The ^{32}P collected in sediment traps at 3 m was only about 40% of the amount necessary to account for losses from the epilimnion other than to the outflow (Table 2). Unexpectedly, whether the traps were below or within the mixed layer did not affect the proportion of lost ^{32}P collected by the traps. Low collection rates indicated that traps were less than 100% efficient, decomposition and phosphorus release took place in the traps during the 6- to 16-d incubations, or mechanisms other than particle settling (e.g. horizontal transport of dissolved and particulate ^{32}P to the lake sides, followed by adsorption or periphyton uptake of the ^{32}P) caused more ^{32}P to be deposited in littoral than in profundal sediments.

Measurement of ^{32}P activity in the sediment cores collected from Lake 227 on 11 October (Table 1) contradicted one of the above hypotheses: ^{32}P was fairly uniformly distributed on the surface of sediments in 0–6 m of water (the extent of the epilimnion at this time). Slightly greater ^{32}P activity was measured for sediments at depths between 6 and 10 m, possibly because some of the ^{32}P in sediments from shallow depths had been resuspended and focused downward.

Assuming that the sediment traps were similarly efficient at all depths, differences in trap catch at 3, 6, and 9 m can be used to estimate the loss of phosphorus from particles to solution during settling. However, the comparison is valid only if corrections are made for the time required for particles to travel the distance between trap depths. The settling rate of particles during our experiment can be calculated from the specific activity of the trapped material, provided that the sediment traps underestimated both radioactive and nonradioactive phosphorus by similar proportions. As shown earlier, the specific activity of small (<10 μm in diameter) particles in the epilimnion of the lake was maximal on the first day of the spike and decreased as new unlabelled phosphorus entered the lake. Therefore, the modal settling velocity of these particles, which normally contained >90% of suspended phosphorus, was equal to trap depth divided by the time required for the particles with the greatest specific activity to reach the trap. The specific activity of particles in traps placed in 3, 6, and 9 m of water was greatest at approximately 1.5, 3, and 5 wk, respectively

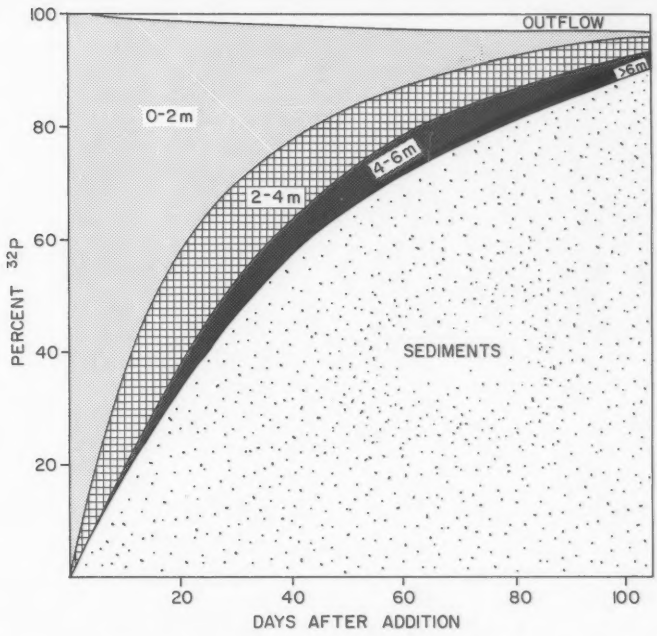


FIG. 7. Partitioning of ^{32}P among water layers, the sediments, and outflow of Lake 227 during the 105 d following ^{32}P addition to the epilimnion. The lines are based on exponential regressions of ^{32}P activity in the particular layers versus time (n = 21).

TABLE 1. ^{32}P activity (±1 SD) in sediment cores collected at various water depths in Lake 227 on day 61 of the whole-lake radiophosphorus study (11 October 1978).

Depth interval (m)	Number of cores	^{32}P (millions cpm·m^{-2})	Sediment area (m^2)	Total ^{32}P (billions cpm)
0–2	4	48.9±17.8	8300	406
1–2	2	78.5±1.1	8700	683
2–4	1	51.3	7000	359
4–6	2	68.2±7.3	7900	539
6–8	2	96.8±17.3	9220	892
8–10	1	88.8	8880	788
Total				3667
Predicted by mass balance				3840

(Fig. 9), suggesting that the modal settling rate of small particles was close to 28 cm·d^{-1}. This value compares well with the "apparent settling velocity" that modellers have used to estimate phosphorus concentration from phosphorus input, 10 m·yr^{-1} (Janus and Vollenweider 1981), or 27 cm·d^{-1} if one presumes that settling rates are constant throughout the year. Particles >10 μm probably settled more quickly than the smaller particles. Some ^{32}P was present in traps collected from 9 m on day 7, indicating that a few particles settled at velocities greater than 1 m·d^{-1}. When the total ^{32}P catch of the 3-m traps is compared with the total radioisotope catch of 6- and 9-m traps 11 and 22 d later (lag time = distance travelled ÷ settling velocity) (Table 2), ^{32}P loss to solution during particle descent

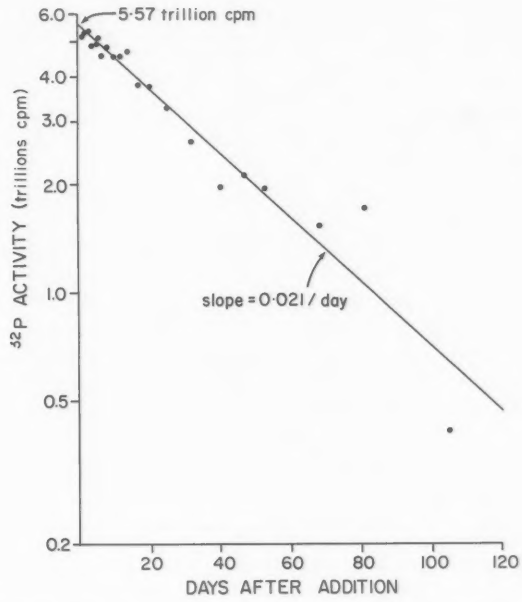


FIG. 8. ^{32}P in the water column of Lake 227 versus days since ^{32}P addition. The line is based on the exponential regression of amount versus time and has the equation $^{32}P = (5.57 \times 10^{12}\ \text{cpm})\ e^{(-0.021 \cdot d^{-1})\ (\text{time})}$, with $r^2 = 0.925$. For unfiltered water samples, 1 cpm was equivalent to 3.072×10^{-9} Bq.

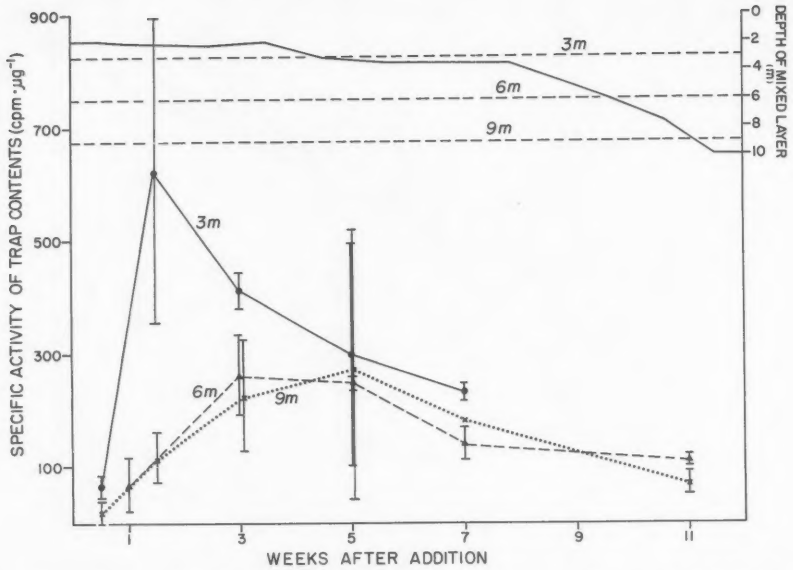


FIG. 9. Specific activity of the contents of sediment traps set at depths of 3, 6, and 9 m in Lake 227 versus time since $^{32}PO_4$ addition to the epilimnion. The depth of the epilimnion is also shown.

TABLE 2. Comparison of the ^{32}P catch of sediment traps with the flux of ^{32}P from the epilimnion. Data are provided for both the period when all traps were below the epilimnion and the greater period between ^{32}P addition and lake overturn (including periods when the 3- and 6-m traps were within the mixed layer).

Sampling period	^{32}P flux from epilimnion (millions cpm · m^{-2})	Trap depth (m)	Number of traps	^{32}P catch in traps (±1 SD) (millions cpm · m^{-2})	Lag-adjusted ^{32}P catch (millions cpm · m^{-2})[a]
11 Aug. to 9 Sept. (epilimnion 3 m deep)	49.2	3	5	19.7±1.5	19.7
		6	4	7.0±1.5	18.2 (to 20 Sept.)
		9	2	5.3±0.6	17.1 (to 31 Sept.)
11 Aug. to 19 Oct. (entire period)	77.4	3	5	33.2±1.3	28.1 (to 27 Sept.)
		6	4	29.7±1.9	24.0 (to 8 Oct.)
		9	2	22.9±1.6	22.9

[a]To adjust for particle travel time between traps (time = travel distance ÷ settling velocity), the 6-m traps are allowed 11 extra days and the 9-m traps 22 extra days to collect ^{32}P. The adjusted collection periods are given in parentheses.

is shown to be low (2−3% · m^{-1}) and similar for the 3- to 6- and 6- to 9-m depth intervals. The residence time of phosphorus in the hypolimnion, calculated by dividing the mean depth of the hypolimnion by the modal settling rate, was 9 d, i.e. much smaller than in the epilimnion.

Return of Phosphorus from Sediments to the Water Column

Despite the general scarcity of ^{32}P in deep water, a minor accumulation of radioactivity in the water directly above hypolimnetic sediments (for our sampling site, 9- to 10-m depth) was evident by day 20 (Fig. 5). By day 81, ^{32}P activity was greater at the bottom of the lake than at any other depth. This distribution of radioisotope suggests that the source of ^{32}P was sediments. To obtain rough estimates of the amount of ^{32}P returned from sediments between the day of ^{32}P addition and various samplings, we multiplied the ^{32}P activity in the 9- to 10-m layer by the volume of water in the lake lying 1 m above sediments. We corrected for ^{32}P contributed by settling particles by subtracting the radioactivity in the upper hypolimnion from the radioactivity in the 9- to 10-m layer. This correction assumed that particles neither disintegrate nor concentrate while settling through the hypolimnion. We have shown that the first assumption is basically correct (<10% of particulate ^{32}P is lost), whereas Schindler and Lean (1974) have shown that the second assumption is untrue for Lake 227, causing our calculations to overestimate ^{32}P feedback from sediments. Our estimates have been additionally exaggerated by the assumption that the sediment−water interactions of the anoxic hypolimnion apply at all sediment surfaces. Despite these limitations, our calculations indicated that only about 4% of the phosphorus settling on 1 m^2 of sediments returned to the water column within 10 wk (Fig. 10). During the first weeks of experimentation, ^{32}P return was much less than 4%, probably because sediment deposition and bacterial colonization involve a lag period.

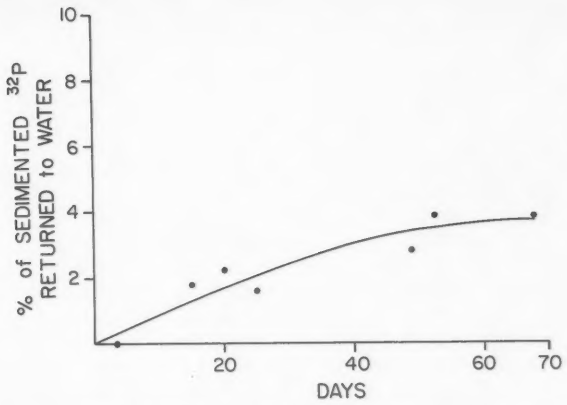


FIG. 10. Fraction of sedimented ^{32}P that returned to the water column of Lake 227 over the first 68 d following ^{32}P addition to the epilimnion. Only data from those days when water samples were taken from 9.5 m are included. The bottom waters were assumed not to mix with overlying waters.

Discussion

A central conclusion can be drawn from our whole-lake study: phosphorus cycling in Lake 227 and perhaps in other phosphorus-limited eutrophic lakes is dominated by the uptake of phosphorus by small particles and their subsequent settling. In excess of 90% of the added $^{32}PO_4$ moved into the sediments of Lake 227 in particles. This affinity of small particles for phosphorus shortens the residence time of the element in the epilimnion, hastens its transport through the hypolimnion and to sediments, and hinders both outflow and uptake by littoral vegetation (chiefly epilithiphyton in Lake 227) as phosphorus sinks.

Phosphorus Cycling in the Epilimnion

For Lake 227, incoming phosphorus is >90% phosphate (chiefly fertilizer) and <5% particulate. If phosphorus remained in phosphate form, it would be susceptible to a number of inorganic reactions, including precipitation with iron and manganese (Stumm and Morgan 1970) and adsorption onto littoral sediments (Syers et al. 1973). However, as our "pre-spike" experiments showed, phosphate is almost wholly incorporated into suspended particles within 10 min of its introduction to the epilimnion. In Lake 227, movement of phosphate to particles can be prevented by biological inhibitors (Levine 1976). Therefore, the process cannot be attributed to abiotic adsorption or chemical precipitation; it must be due to active biological uptake. Despite phosphate fertilizer additions, orthophosphate concentrations in the epilimnion of Lake 227 remain very low. Reliable methods for orthophosphate measurement do not exist for Canadian Shield lakes (Stainton 1980), but radiobioassays for orthophosphate performed during the summers of 1973 and 1974 yielded estimates of 1−50 ng $PO_4 \cdot L^{-1}$ (Levine and Schindler 1980). We can obtain an estimate of phosphate-P concentration during our experiments by multiplying total phosphorus concentration by the quotient (^{32}P in the <1000 molecular weight fraction)/(total ^{32}P). Because no ^{32}P was detected in the <1000 molecular weight fraction, we substituted for this quantity the limit of detection for ^{32}P relative to background activity. The maximum estimate obtained by this calculation was 250 ng PO_4-$P \cdot L^{-1}$, an amount too low to support substantial inorganic chemical activity.

Identification of the particles responsible for phosphate uptake is important. The morphology of the organisms involved may affect the subsequent passage of phosphorus up food chains, while size affects the rapidity of phosphorus sedimentation. For Lake 227, we found that particles between 0.2 and 10 μm in diameter performed >95% of phosphate uptake. Several limnologists (Rigler 1956; Rhee 1972; Burnison 1975; Currie and Kalff 1984) have hypothesized that bacteria dominate phosphate uptake in lakes, but we could not confirm this hypothesis for Lake 227. In both short-term (10 min) experiments in beakers and during the long-term whole-lake experiment, the 1- to 10-μm size fraction took up three times as much ^{32}P as the 0.2- to 1-μm fraction and had a similar specific activity after 10 min of exposure to $^{32}PO_4$. In 1974, similar short-term experiments with lake water from Lake 227 (Levine 1976) showed domination of radiophosphate uptake by particles 3−10 μm in diameter. Although a filter with 1-μm pores does not completely separate bacteria and phytoplankton, biweekly phytoplankton counts during the experiment indicated that the bulk of phytoplankton should have appeared in the 1- to 10-μm pool: >50% of the phytoplankton biomass was in cells with their largest linear dimensions between 1 and 10 μm, and another 15−30% of phytoplankton biomass was in cells with some linear dimensions <10 μm, so that correctly aligned cells could pass through a 10-μm filter (D. Findlay, unpubl. data). On the other hand, bacteria with linear dimensions >0.5 μm were rare. Therefore, uniform labelling of the 0.2- to 10-μm compartments indicates either that small phytoplankton were able to take up reasonable amounts of $^{32}PO_4$ directly, despite competition with bacteria, or that indirect labelling of phytoplankton with ^{32}P is extremely rapid. Currie and Kalff (1984) have recently proposed that natural phytoplankton use the dissolved organic phosphorus (DOP) excreted by bacteria as a primary phosphorus source, because they cannot compete with bacteria for phosphate. If this is the case in Lake 227, the flow of phosphorus from dissolved phosphate to bacteria to DOP to phytoplankton must occur in <3 min. If the flow were significantly slower, the two particulate phosphorus pools would not have similar specific activities after 10 min (for an exponential function, 95% of the receiving pool is replaced by the exchanged substance in three flushings). We suspect that the relative importance of phosphate and DOP as sources of phosphorus for small phytoplankton is related to the abundance of bacteria in the euphotic zone, a parameter that varies from lake to lake.

Radiophosphorus assimilation into larger phytoplankton and into zooplankton was relatively slow. During our whole-lake experiment, less than 5% of ^{32}P was incorporated into particles >10 μm in diameter. Low passage of phosphorus "up the food chain" was partly a function of the much smaller size of pools in the larger size categories (Fig. 2), but slow phosphorus turnover by the large plankton was also a factor. The latter phenomenon was apparent from the extremely slow increases in specific activity that were observed for the >10-μm fraction. If the small quantity of ^{32}P in large particles was due to simultaneous high uptake and losses, the large particles would have reached equilibrium specific activities much more rapidly than they did.

Lean and White (1983) have recently shown that the relative importance of large and small particles in $^{32}PO_4$ uptake varies with phosphate concentration. In Jacks Lake, Ontario, particles 0.2−1 μm in diameter dominated $^{32}PO_4$ uptake at low phosphate concentrations (<1 $\mu g \cdot L^{-1}$), while particles >5 μm in diameter dominated uptake at phosphate concentrations in excess of 5 $\mu g \cdot L^{-1}$. Given these findings, one may question whether our $^{32}PO_4$ addition traced the normal fate of phosphate in Lake 227. We spread radiotracer over the lake surface, while phosphate fertilizer entered the lake at a single point, perhaps creating a temporary microenvironment with high phosphate concentrations. Could most of the phosphate uptake in Lake 227 be by large phytoplankton, despite our findings that >95% of $^{32}PO_4$ was incorporated into microplankton? We believe not, firstly because much more nonradioactive phosphorus was present in microplankton than in particles >10 μm in diameter, suggesting microplankton success, and secondly because the larger plankton take up phosphate very slowly (at a rate of about 1 $\mu g \cdot L^{-1} \cdot h^{-1}$ according to Lean and White (1983)) whereas the mixing of phosphate and phytoplankton cells within the epilimnion is relatively rapid. Finally, the predominant source of phosphate for phytoplankton in the epilimnion of Lake 227 is not external supply, but recycling (Levine and Schindler 1980), which occurs throughout the epilimnion rather than at a single site.

Some phosphorus leaves particles through cellular excretion and lysis. This phosphorus may be reused or left in solution, depending on its bioavailability. In concurrence with the results of earlier studies of DP in Lake 227 (Schindler and Lean 1974; Levine and Schindler 1980), we found that little of "dissolved" phosphorus is phosphate and much is colloidal (molecular weight >100 000). In addition, our data on the specific activity of DP indicated that the DP fraction contains both exchangeable and inactive phosphorus. The exchangeable and inactive pools of DP appear to be roughly equal in size, but widely divergent in behavior. Whereas the exchangeable pool of DP attained isotopic steady state within 2−3 d of radiophosphate addition, the "inactive" pool acquired ^{32}P so slowly that, at the time scale of most fluxes in the internal phosphorus cycle, it can be considered as functionally inert. The relative activity of the two DP pools may be related to their vulnerability to phosphatases. Downes and Paerl (1978) and White et al. (1981) have provided evidence for labile and inactive pools of high molecular weight DP in New Zealand lakes and in Canadian lakes not on the Precambrian Shield.

Phosphorus Exchange Between the Epilimnion and Littoral Zone

Water in the thermocline region of thermally stratified small lakes moves relatively rapidly along horizontal planes and slowly in the vertical direction (Quay 1977). Our vertical profiles indicated just how strong a barrier to mixing the thermocline in Lake 227 was: almost no detectable dissolved ^{32}P moved into deep water during the period of lake stratification. Because incoming dissolved materials are confined to the epilimnion, there are ample opportunities for the dissolved substances in a small lake to interact with sediment and biota in the littoral zone.

Two whole-lake radiotracer experiments in the ELA lakes, one with ^{226}Ra and the other with heavy metal radioisotopes, have shown enhanced deposition of radioisotope in the littoral zone as a result of the adsorption of free ions onto sediments. Adsorption was implicated by (1) a significant and positive relationship between the proportion of radiotracer taken up by littoral sediments and the proportion of radiotracer lost from solution (Hesslein et al. 1980) and (2) failure by biological poisons to inhibit ^{226}Ra uptake by sediments (Emerson and Hesslein 1973).

In previous whole-lake radiophosphorus experiments, direct measurements of ^{32}P loss to the littoral zone were not made. However, in lakes bordered with macrophytes, large discrepancies appeared between the amount of ^{32}P lost from the open water and the amount of ^{32}P measured in the outflows and hypolimnetic sediments of these lakes (Coffin et al. 1949; Hayes et al. 1952; Rigler 1956; Chamberlain 1968), suggesting that littoral deposition was a major phosphorus sink. For example, Rigler (1956) estimated that the flux of phosphorus from the epilimnion to the littoral zone in Toussaint Lake, Ontario, was five times as great as the flux of phosphorus to the hypolimnion via sedimentation. On the other hand, in Linsley Pond, a lake with few macrophytes, ^{32}P moved predominantly downward, in a manner similar to that observed in Lake 227 (Hutchinson and Bowen 1950).

In Lake 227, there was no convincing evidence for significant phosphorus exchange at the littoral−epilimnion interface, beyond the particle deposition common to the whole lake. Radiophosphorus exchange between open water and littoral sediments was no greater than sediment−water exchange at any other depth. The kinetics of ^{32}P loss from Lake 227 were monophasic, not diphasic as others have observed when radiophosphate was added to macrophyte-rich lakes. Monophasic ^{32}P loss also occurred in macrophyte-poor Linsley Pond (Rigler 1973). In brief, it appears that monophasic movement of phosphorus is characteristic of lakes where macrophytes are rare, because almost all phosphorus losses occur via sedimenting particles.

Substantial adsorption of phosphorus by littoral sediments was not expected because phosphorus was almost entirely in particles, rather than as phosphate ion. In addition, uptake by macrophytes was not expected because macrophytes are scarce in Lake 227. High exchange of phosphorus between open water and the littoral zone must require either high phosphate concentrations, a situation that develops only in certain highly eutrophic lakes, or an abundance of macrophytes.

Phosphorus Exchange Between the Epilimnion and Hypolimnion

About one half of the phosphorus input to Lake 227 is carried into the hypolimnion in sinking particles, while the other half settles onto epilimnetic or metalimnetic sediments. The rate of ^{32}P sedimentation from the epilimnions of small lakes appears to be rather constant: loss rates of 1−3% of $^{32}P \cdot d^{-1}$ were measured during both the Lake 227 and earlier whole-lake radiophosphorus experiments (Rigler 1973), during radiophosphorus experiments in in situ enclosures (Charlton 1975; Lean et al. 1975), and in mass balance studies where sedimentation could be calculated because other budget terms were precisely known (Schindler et al. 1973).

Perhaps the most interesting result of our study was the illustration that the phosphorus "cycle" in the hypolimnion is primarily a throughflow system. Low release of dissolved phosphorus from settling particles was implicated by differences in sediment trap catch at 3, 6, and 9 m, which showed about 10% loss of radiophosphorus from particles to solution

during settling through the entire length of the hypolimnion (5–10 m). In addition, the modal settling velocity of particulate phosphorus, 28 $cm \cdot d^{-1}$, was close to the settling velocities of microplankton in cylinders in the laboratory (Oliver et al. 1981). Any time that phosphorus spends in solution in the hypolimnion should reduce the modal settling velocity of the element relative to the settling velocity of whole cells. However, eventually, much of the ^{32}P released to solution in the hypolimnion must have been reincorporated into particles and its journey to the sediments renewed, for mass balance calculations showed that less than 1% of the ^{32}P that had entered the hypolimnion between August and October remained in the water in late October. That microbes in the anoxic hypolimnion of Lake 227 take up radiophosphate has been shown by Schindler and Lean (1974) and Levine and Schindler (1980). The combination of gradual ^{32}P loss from the epilimnion and short hypolimnetic residence time explains the small amount of ^{32}P in the hypolimnion at any one time. The increased concentration of nonradioactive phosphorus near the bottom in Lake 227 is not an accurate reflection of the fate of the phosphorus supplied at the lake's surface, because particles concentrate with depth due to decreasing water volume with increasing depth, and because there was accumulated dissolved phosphorus at depths where tha lake had not mixed since the fall of 1977 or earlier.

Low phosphorus recycling in the hypolimnion is probably a function of the rapid death and autolysis of cells while still in the epilimnion (Ohle 1965). By the time detritus reaches the hypolimnion, its remaining phosphorus content is largely refractory and especially difficult to degrade under anoxic conditions. The carbon and trace metals in detritus also appear to be largely refractory, although perhaps less so than detrital phosphorus: 1- to 10-μm particulate organic carbon in water in in situ chambers settled at a mean rate of 24 $cm \cdot d^{-1}$ (Burns and Rosa 1980), while metal-radiolabelled particles in ELA Lake 224 settled at a mean velocity of 18 $cm \cdot d^{-1}$ (Hesslein et al. 1980).

Phosphorus cycling in the hypolimnion of Lake 227 is additionally retarded by low rates of input of dissolved phosphorus. As discussed earlier, the thermocline prevents the intrusion of dissolved phosphorus from the epilimnion. While phosphate return from sediments may fuel phosphorus cycling in the hypolimnions of some lakes (Wetzel 1983), the sediments of Lake 227 seem to adsorb nearly all of the phosphorus released into porewater during decomposition (Schindler et al. 1977). Phosphorus, apparently bound as humic–metal–phosphorus complexes (Jackson and Schindler 1975), is retained by sediments even under prolonged anoxia. Less than 5% of the ^{32}P that reached the sediment surface of Lake 227 between 11 August and 7 November 1978 returned to the water column before 7 November.

Lakes with phosphorus-limited phytoplankton and low to moderate flushing rates are typified by high phosphorus retention (>80% of input) (Vollenweider 1975). For Lake 227, we have shown that high phosphorus retention (>95% of added ^{32}P) is the end product of three phenomena: the high affinity of small particles for phosphorus regardless of whether oxic or anoxic conditions prevail, the inevitable sedimentation of these particles, and very low phosphorus release from sediments.

Acknowledgments

We thank G. Goodwin, G. Regier, R. Schade, and S. Prychitko for technical assistance. D. Findlay supplied phytoplankton data for the period of study. P. Campbell, E. J. Fee, F. P. Healey, R. Hecky, R. Hesslein, K. Limburg, S. Tarapchak, and two anonymous reviewers provided valuable criticism of the manuscript. This work was supported by the Canadian Department of Fisheries and Oceans. The senior author also acknowledges support during manuscript preparation from the U.S. Environmental Protection Agency under Cooperative Agreement CR 811060 to Cornell University.

References

BROWN, L. C. 1971. Determination of phosphorus-32 and phosphorus-33 in aqueous solution. Anal. Chem. 43: 1326–1328.

BRUNSKILL, G. J., D. POVOLEDO, B. W. GRAHAM, AND M. P. STAINTON. 1971. Chemistry of surface sediments of sixteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 277–294.

BRUNSKILL, G. J., AND D. W. SCHINDLER. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

BURNISON, K. B. 1975. Microbial ATP studies. Int. Ver. Theor. Angew. Limnol. Verh. 19: 286–290.

BURNS, N. M., AND F. ROSA. 1980. In situ measurement of the settling velocity of organic carbon particles and 10 species of phytoplankton. Limnol. Oceanogr. 25: 855–864.

CHAMBERLAIN, W. M. 1968. A preliminary investigation of the nature and importance of soluble organic phosphorus in the phosphorus cycle of lakes. Ph.D. thesis, University of Toronto, Toronto, Ont. 232 p.

CHANG, P. S. S., D. F. MALLEY, W. J. FINDLAY, G. MUELLER, AND R. T. BARNES. 1980. Species composition and seasonal abundance of zooplankton in Lake 227, Experimental Lakes Area, northwestern Ontario, 1969–1978. Can. Data Rep. Fish. Aquat. Sci. 182: iv + 101 p.

CHARLTON, M. N. 1975. Sedimentation: measurements in experimental enclosures. Int. Ver. Theor. Angew. Limnol. Verh. 19: 267–272.

COFFIN, C. C., F. R. HAYES, L. H. JODREY, AND S. G. WHITEWAY. 1949. Exchange of materials in a lake as studied by the addition of radioactive phosphorus. Can. J. Res. Sect. D 27: 207–222.

CRUIKSHANK, D. R. 1984. Whole lake chemical additions in the experimental Lakes Area. 1969–1983. Can. Data Rep. Fish. Aquat. Sci. 449: iv + 23 p.

CURRIE, D. J., AND J. KALFF. 1984. The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in freshwater. Limnol. Oceanogr. 29: 311–321.

DOWNES, M. T., AND H. W. PAERL. 1978. Separation of two dissolved reactive phosphorus fractions in lakewater. J. Fish. Res. Board Can. 35: 1636–1639.

EMERSON, S., AND R. H. HESSLEIN. 1973. Distribution and uptake of artificially introduced radium-226 in a small lake. J. Fish. Res. Board Can. 30: 1485–1490.

FINDLAY, D. L. 1981. Seasonal successions of phytoplankton in seven lake basins in the Experimental Lakes Area, northwestern Ontario, following artificial eutrophication. Data from 1977 to 1979. Can. MS Rep. Fish. Aquat. Sci. 1627: iv + 40 p.

HAYES, F. R., J. A. MCCARTER, M. L. CAMERON, AND D. A. LIVINGSTONE. 1952. On the kinetics of phosphorus exchange in lakes. J. Ecol. 40: 202–216.

HEANEY, S. I. 1974. A pneumatically-operated water sampler for close intervals of depth. Freshwater Biol. 4: 103–106.

HESSLEIN, R. H., W. S. BROECKER, AND D. W. SCHINDLER. 1980. Fates of metal radiotracers added to a whole lake: sediment–water interactions. Can. J. Fish. Aquat. Sci. 37: 378–386.

HUTCHINSON, G. E., AND V. T. BOWEN. 1947. A direct demonstration of the phosphorus cycle in a small lake. Proc. Natl. Acad. Sci. USA. 33: 148–153.

1950. A quantitative radiochemical study of the phosphorus cycle in Linsley Pond. Ecology 31: 194–203.

JACKSON, T. A., AND D. W. SCHINDLER. 1975. The biogeochemistry of phosphorus in an experimental lake environment: evidence for the formation of humic–metal–phosphorus complexes. Int. Ver. Theor. Angew. Limnol. Verh. 19: 211–221.

JANUS, L. L., AND R. A. VOLLENWEIDER. 1981. Summary Report. The OECD Cooperative Programme on Eutrophication. Can. Contrib. Sci. Ser. No. 131. National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ont.

LEAN, D. R. S., M. N. CHARLTON, B. K. BURNISON, T. P. MURPHY, G. E. MILLARD, AND K. R. YOUNG. 1975. Phosphorus: changes in ecosystem

metabolism from reduced loading. Int. Ver. Theor. Angew. Limnol. Verh. 19: 249–257.

LEAN, D. R. S., AND E. WHITE. 1983. Chemical and radiotracer measurements of phosphorus uptake by lake plankton. Can. J. Fish. Aquat. Sci. 40: 147–155.

LEVINE, S. 1975. Orthophosphate concentration and flux within the epilimnia of two Canadian Shield lakes. Int. Ver. Theor. Angew. Limnol. Verh. 19: 624–629.

LEVINE, S. N. 1976. A preliminary investigation of orthophosphate concentration and the uptake of orthophosphate by seston in two Canadian Shield lakes. M.Sc. thesis, University of Manitoba, Winnipeg, Man. 151 p.

LEVINE, S. N., AND D. W. SCHINDLER. 1980. Radiochemical analysis of orthophosphate concentration and seasonal changes in the flux of orthophosphate in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 335–341.

NEWBURY, R. W., AND K. G. BEATY. 1980. Water renewal efficiency of watershed and lake combinations in the ELA region of the Precambrian Shield. Can. J. Fish. Aquat. Sci. 27: 335–341.

OHLE, W. 1965. Primarproduktion des phytoplanktons und Bioaktivitiat holsteinischer Seen. Methoden und Ergebnisse, p. 24–43. *In* Limnologie Symposium, Helsinki, 1964.

OLIVER, R. L., A. J. KINNEAR, AND G. G. GANF. 1981. Measurements of cell density of three freshwater phytoplankters by density gradient centrifugation. Limnol. Oceanogr. 26: 285–294.

QUAY, P. D. 1977. An experimental study of turbulent diffusion in lakes. Ph.D. thesis, Columbia University, New York, NY. 194 p.

RHEE, G.-Y. 1972. Competition between an alga and an aquatic bacterium for phosphate. Limnol. Oceanogr. 17: 505–514.

RIGGS, D. S. 1963. The mathematical approach to physiological problems. M.I.T. Press, Cambridge, MA. 445 p.

RIGLER, F. H. 1956. A tracer study of the phosphorus cycle in lake water. Ecology 37: 550–561.

1973. A dynamic view of the phosphorus-cycle in lakes, p. 539–573. *In* E. Griffith, A. Beeton, J. Spencer, and D. Mitchell [ed.] Environmental phosphorus handbook. Wiley Interscience, New York, NY.

SCHINDLER, D. W. 1971. Carbon, nitrogen, and phosphorus and the eutrophication of freshwater lakes. J. Phycol. 7: 321–329.

1975. Whole-lake eutrophication experiments with phosphorus, nitrogen, and carbon. Int. Ver. Theor. Angew. Limnol. Verh. 19: 3221–3231.

1985. The coupling of biogeochemical cycles by organisms: evidence from whole-lake chemical perturbations, p. 225–250. *In* W. Stumm [ed.] Chemical processes in lakes. John Wiley & Sons, New York, NY.

SCHINDLER, D. W., F. A. J. ARMSTRONG, S. K. HOLMGREN, AND G. J. BRUNSKILL. 1971. Eutrophication of Lake 227, Experimental Lakes Area, northwestern Ontario, by addition of phosphate and nitrate. J. Fish. Res. Board Can. 28: 1763–1782.

SCHINDLER, D. W., R. H. HESSLEIN, AND G. KIPPHUT. 1977. Interactions between sediments and overlying waters in an experimentally eutrophied Precambrian Shield lake, p. 235–243. *In* H. L. Golterman [ed.]. Interactions between sediments and freshwater. Junk, The Hague.

SCHINDLER, D. W., H. KLING, R. V. SCHMIDT, J. PROKOPOWICH, V. E. FROST, R. A. REID, AND M. CAPEL. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

SCHINDLER, D. W., AND D. R. S. LEAN. 1974. Biological and chemical mechanisms in the eutrophication of freshwater lakes. Ann. N.Y. Acad. Sci. 250: 129–135.

SCHINDLER, D. W., D. R. S. LEAN, AND E. J. FEE. 1975. Nutrient cycling in freshwater ecosystems, p. 96–105. *In* D. R. Reichle [ed.] Productivity of world ecosystems. U.S. National Academy of Sciences, Washington, DC.

STAINTON, M. P. 1980. Errors in molybdenum blue methods for determining orthophosphate in freshwater. Can. J. Fish. Aquat. Sci. 37: 472–478.

STAINTON, M. P., M. J. CAPEL, AND F. A. J. ARMSTRONG. 1977. The chemical analysis of freshwater. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25 (2nd ed.): 180 p.

STUMM, W., AND J. MORGAN. 1970. Aquatic chemistry. Wiley-Interscience, London. 780 p.

SYERS, J. K., R. F. HARRIS, AND D. E. ARMSTRONG. 1973. Phosphate chemistry in lake sediments. J. Environ. Qual. 2: 1–14.

VOLLENWEIDER, R. A. 1975. Input–output models with special reference to the phosphorus loading concept in limnology. Schweiz. Z. Hydrol. 37: 53–84.

WETZEL, R. G. 1983. Limnology. Saunders, New York, NY. 767 p.

WHITE, E., G. PAYNE, S. PICKMERE, AND F. R. PICK. 1981. Orthophosphate and its flux in lake waters. Can. J. Fish. Aquat. Sci. 38: 1215–1219.

Identification of Critical Nutrient Levels through Field Verification of Models for Phosphorus and Phytoplankton Growth[1]

Martin T. Auer

Department of Civil Engineering and Department of Biological Sciences, Michigan Technological University, Houghton, MI 49931, USA

Mark S. Kieser[2]

Department of Biological Sciences, Michigan Technological University, Houghton, MI 49931, USA

and Raymond P. Canale

Department of Civil Engineering, University of Michigan, Ann Arbor, MI 48109, USA

Auer, M. T., M. S. Kieser, and R. P. Canale. 1986. Identification of critical nutrient levels through field verification of models for phosphorus and phytoplankton growth. Can. J. Fish. Aquat. Sci. 43: 379–388.

Two models for phosphorus and phytoplankton growth were field verified along a marked gradient in trophic conditions in Green Bay (Lake Michigan): one, the Monod model, relates growth rate to external (dissolved) phosphorus concentration, and the other, the Droop model, describes growth rate as a function of internal (stored) phosphorus levels. The verification provided through a satisfactory fit of model output to field measurements of phosphorus and gross photosynthesis established a conceptual foundation for empirical models relating phosphorus and trophic state parameters. Phosphorus concentrations corresponding to boundary conditions for trophic state categories were developed based on the verified models by defining oligotrophy as the region of linear response by growth rate to increases in phosphorus (<1.2 μg soluble reactive phosphorus (SRP)·L^{-1}, <11.5 μg total phosphorus (TP)·L^{-1}), mesotrophy as the transitional state (1.2–8.0 μg SRP·L^{-1}, 11.5–37.5 μg TP·L^{-1}), and eutrophy as the region where growth rate is saturated, i.e. insensitive to changes in phosphorus concentration (>8.0 μg SRP·L^{-1}, >37.5 μg TP·L^{-1}). We applied the trophic state classification scheme to several Great Lakes basins to examine their sensitivity to changes in phosphorus levels. The oligotrophic waters of Lakes Superior, Huron, and Michigan and northern Green Bay and Georgian Bay have the greatest sensitivity to increases in total phosphorus concentration. The eutrophic waters of southern Green Bay, western Lake Erie, and nearshore Lake Ontario are nutrient saturated and relatively insensitive to initial reductions in phosphorus levels. Offshore Lake Ontario, eastern and central Lake Erie, Saginaw Bay, and mid Green Bay lie in the transitional phase for sensitivity to phosphorus management.

Deux modèles établissant une relation entre le phosphore et le taux de croissance du phytoplancton ont été vérifiés sur le terrain le long d'un gradient marqué des conditions trophiques dans la baie Green (lac Michigan). Le premier modèle, le modèle de Monod, établit une relation entre le taux de croissance et la concentration de phosphore externe (dissous), le second, le modèle de Droop, décrit le taux de croissance en fonction de la teneur interne en phosphore (emmagasiné). La vérification, comportant un ajustement satisfaisant des résultats de la modélisation aux teneurs en phosphore et aux valeurs de la photosynthèse brute déterminées sur le terrain, peut servir de base à l'élaboration de modèles empiriques de relations entre le phosphore et les paramètres de l'état trophique. Les concentrations de phosphore correspondant aux conditions limites des catégories des états trophiques ont été établies à partir des modèles vérifiés, avec définition de l'oligotrophie comme la zone de réponse linéaire du taux de croissance à l'augmentation de la teneur en phosphore (<1,2 μg de phosphore réactif soluble (PRS)·L^{-1}, <11,5 μg de phosphore total (PT)·L^{-1}), la mésotrophie comme la zone de transition (1,2–8,0 μg PRS·L^{-1}, 11,5–37,5 μg PT·L^{-1}) et l'eutrophie comme la zone de saturation du taux de croissance, c'est-à-dire la zone où le taux demeure insensible aux variations de la concentration du phosphore (>8,0 μg PRS·L^{-1}, >37,5 μg PT·L^{-1}). Nous avons appliqué cette classification de l'état trophique à plusieurs bassins des Grands Lacs pour en étudier la sensibilité aux variations de la concentration du phosphore. Les eaux oligotrophes des lacs Supérieur, Huron et Michigan, du nord de la baie Green et de la baie Georgienne sont les plus sensibles aux augmentations de la concentration de phosphore total. Les eaux eutrophes du sud de la baie Green, de l'ouest du lac Érié et de la zone riveraine du lac Ontario sont saturées en matières nutritives et relativement insensibles au premières réductions des concentrations de phosphore. Les eaux du large du lac Ontario, des parties est et centrale du lac Érié, de la baie Saginaw et de la partie centrale de la baie Green se situent dans la phase de transition en ce qui concerne la sensibilité à la lutte contre le phosphore.

Received November 30, 1984
Accepted August 13, 1985
(J8039)

Reçu le 30 novembre 1984
Accepté le 16 août 1985

The evolution of limnology and aquatic ecology from their earlier descriptive stage to the current focus on quantification of dynamic phenomena such as phytoplankton growth kinetics has been accompanied by an increased reliance on mathematical models. Models vary from simple linear or log-linear functions such as that developed for

[1] This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

[2] Current address: LTI, Limno-Tech, Inc., 15 Research Drive, Ann Arbor, MI 48103, USA.

phosphorus and chlorophyll by Dillon and Rigler (1974) to more complex nutrient – food web models (e.g. Bierman and Dolan 1981). Simple models offer great ease of application, but may not accurately or adequately represent the mechanisms driving nutrient-limited phytoplankton growth. Complex models provide a comprehensive description of the system, but may include many coefficients for which no applicable or reliable estimates are available. It is important to seek levels of system description and data requirement which afford ease of application as well as a high degree of model credibility.

The basic premise of the research described here is that the practical application of models for the simulation of phosphorus-limited phytoplankton growth is restricted because most existing models are either too simple to be realistic (or mechanistically satisfying) or too complex to be reliably applied. We tested the hypothesis that growth by natural phytoplankton assemblages, as a function of phosphorus availability, may be described by accepted physiological models using average values for the key nutrient-related growth coefficients. DiToro and Connolly (1980) successfully applied an average apparent half-saturation constant for phosphorus and growth by the natural phytoplankton assemblage in a study of Lake Erie. Jannasch (1974), however, suggested that long-term exposure of natural phytoplankton populations to any nutrient concentration would result in changes in population structure and physiology that could not be described by average growth or uptake constants. We examined the applicability of average values for kinetic coefficients by providing field verification of two physiological models using natural assemblages of phosphorus-limited phytoplankton along a striking gradient in phosphorus, phytoplankton biomass, and primary production in Green Bay, Lake Michigan.

Models for Phytoplankton Growth

Mass balance models for phytoplankton population dynamics include rate terms for growth, respiration loss, settling loss, and grazing loss. The net change in population biomass is calculated as the gross specific growth rate less the three loss rate terms. The gross specific growth rate is a fraction of the maximum gross specific growth rate calculated using dimensionless functions which describe the response of the algal population to variations in light, temperature, and nutrient abundance:

$$(1) \quad \mu = \mu_{max} \cdot (F_I, F_T, F_N)$$

where μ = gross specific growth rate (time^{-1}), μ_{max} = maximum gross specific growth rate (time^{-1}), F_I = a function relating growth and light intensity, F_T = a function relating growth and temperature, and F_N = a function relating growth and nutrient availability.

Two basic kinetic formulations (F_N) relating substrate or nutrient availability and microbial growth have been applied to the study of algal population dynamics. Monod (1942) related growth rate to the external or dissolved substrate concentration according to the following expression:

$$(2) \quad F_N = S/(K_s + S)$$

where S = substrate concentration (mass · volume^{-1}) and K_s = half-saturation constant for growth as a function of substrate concentration (mass · volume^{-1}). A plot of growth rate versus substrate concentration for the Monod model yields a rectangular hyperbola with growth rate increasing from zero with no substrate present and asymptotically approaching the maximum specific growth rate at saturating substrate levels. The half-saturation constant, K_s, is defined as the substrate concentration at which one half the maximum specific growth rate is achieved. The Monod model has been successfully applied to the study of resource-based competition for two species of freshwater diatoms in laboratory culture (Tilman and Kilham 1976). The Monod model was developed for organisms with a steady-state physiology, i.e. growing in the presence of an invariant substrate concentration. The model does not address the phenomenon of luxury uptake, nor does it address the substantial spatial and temporal heterogeneity observed for both nutrients and phytoplankton biomass in natural systems. The Monod model is thus criticized as providing an incomplete representation of the mechanisms driving phytoplankton–nutrient dynamics.

Droop (1968) recognized the importance of luxury uptake in relating growth rate to internal (stored) nutrient pool size or cell quota:

$$(3) \quad F_N = 1 - (Q_0/Q)$$

where Q = cell quota (mass nutrient · cell biomass^{-1}) and Q_0 = minimum cell quota (mass nutrient · cell biomass^{-1}). The Droop model also yields a rectangular hyperbola, with zero growth at the minimum cell quota (a value >0) and asymptotically approaching the maximum specific growth rate at high cell quotas. The utility of the Droop model has been verified for laboratory cultures of *Anabaena wisconsinense* and *Chlorella pyrenoidosa* (Senft 1978) and field populations of *Cladophora glomerata* (Auer and Canale 1982). The major drawback to the Droop model is that it describes growth as a direct characteristic of the cell's physiology, which is only an indirect reflection of the cell's external environment. Management application of the model requires that growth be linked to the external environment by conducting a mass balance on internal nutrient pool size, considering contributions to the internal pool through nutrient uptake and losses from the pool through the demand for growth. The increased complexity required to accommodate nutrient uptake kinetics reduces the ease of application and thus the utility of the Droop model. DiToro (1980) recognized this problem in developing a phytoplankton–nutrient model for Lake Erie. DiToro argued that since gains through the nutrient uptake process occur rapidly relative to losses through the demand for growth, cells are in equilibrium with their external environment when the rate of change in substrate concentration is slow relative to the rate of growth. Thus the response of phytoplankton growth rates (time frame of days) to seasonal variation in nutrient availability (time frame of weeks) may be appropriately characterized by the simpler Monod model. Successful field verification of these models for phosphorus and phytoplankton growth would indicate that results obtained using the easily applied Monod model are consistent with results that would be obtained using the more complex, but mechanistically satisfying Droop model.

Materials and Methods

Water samples were collected 1 m below the surface and 1 m above bottom over a network of stations (Fig. 1) on 18 cruises between 25 May and 6 October 1982. Water temperature profiles and Secchi disk transparency measurements were made at each station. Light profiles were taken at stations on the east side of the bay using a Li-Cor meter and spherical

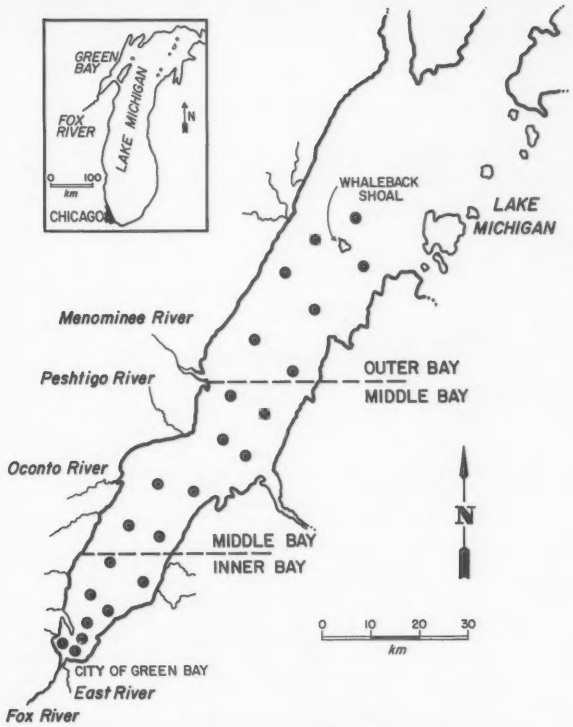


FIG. 1. Morphology of Green Bay, location of sampling stations, and orientation of the bay with respect to Lake Michigan.

quantum sensor (model LI-185A), and the vertical extinction coefficient was calculated as described by Lind (1979). Water samples were divided into four aliquots: (1) unfiltered and frozen for total phosphorus (TP) and total organic carbon (TOC) analysis, (2) filtered (0.45 μm) and frozen for dissolved phosphorus and dissolved organic carbon (DOC) analysis, (3) buffered, filtered (0.45 μm), and filters frozen for chlorophyll *a* analysis, and (4) unfiltered, stored in a cool ice chest for seston dry weight and primary production measurements.

Chlorophyll *a* and phaeophytin were extracted with dimethylsulfoxide (DMSO) according to the method of Burnison (1980) and measured spectrophotometrically. TOC and DOC were measured using an Ionics model 1258M TOC-TC analyzer; particulate organic carbon (POC) was obtained by difference. Soluble reactive phosphorus (SRP) and total dissolved (persulfate digestion) phosphorus (TDP) were measured spectrophotometrically (10 cm cell) using the ascorbic acid technique (APHA 1980). TP was measured in an identical fashion on unfiltered samples following persulfate digestion; particulate phosphorus (PP) was obtained by difference. Seston dry weight was obtained by filtering 1 L of sample through a glass fiber filter (Whatman GF/C) and measuring the filter's weight gain after drying at 103°C. Gross photosynthesis was measured using the light-bottle/dark-bottle (oxygen evolution) technique (Vollenweider 1969). Samples were incubated at 20°C for 12 h in the light (200 $\mu E \cdot m^{-2} \cdot s^{-1}$) and 12 h in the dark. Changes in dissolved oxygen were measured using an Orion Instruments model 97-08 oxygen electrode and Orion Instruments model 501 digital meter. Gross photosynthesis (mg $O_2 \cdot L^{-1} \cdot d^{-1}$) was calculated as the sum of net photosynthesis and respiration.

Model coefficients were derived statistically using PAR, a derivitive-free nonlinear regression technique (Ralston 1983). Goodness of fit was compared among models using a measure of the relative variation between model output and data analagous to the coefficient of variation:

$$(4) \quad CV = [E/y] \cdot 100$$

where CV = coefficient of variation (%), E = mean error = (mean square error)$^{0.5}$, and y = mean value for the dependent variable. Expression of goodness of fit in this way provides an estimate of variation that is independent of the scale of measurement, e.g. different expressions of specific growth rate.

The Green Bay System

Green Bay is a major gulf located in the northwest corner of Lake Michigan (Fig. 1) and is often cited as one of the major water quality problem areas in the Great Lakes. Historically, industrial discharges from the pulp and paper industry, municipal discharges from wastewater treatment plants, and agricultural runoff have contributed to dissolved oxygen depletion, excessive algal growth, reduced water clarity, and taste and odor problems in the bay.

Green Bay has a length along its major northeast–southwest axis of 160 km, a mean width of 22 km, a mean depth of 15.8 m, holds approximately 67 km^3 of water, and has a mean residence time of 6 yr (Mortimer 1978). According to the typologies of Chapra and Dobson (1981), trophic state in Green Bay varies from eutrophic (or hypereutrophic) in the extreme lower bay near the city of Green Bay to oligotrophic conditions near the bay's junction with Lake Michigan, approximately 120 km to the north. The Fox River is the single greatest hydrologic and pollutant source for Green Bay, contributing 45% of the total flow and 78% of the total phosphorus loading (Roznowski and Auer 1984); this amounts to approximately 10% of the total phosphorus input to Lake Michigan (Sager and Wiersma 1972; Sonzogni et al. 1978).

Perhaps the most striking feature of the system is the strong gradient in water quality and trophic conditions established along the major axis of the bay in response to the Fox River discharge. The gradient in trophic characteristics is summarized in Fig. 2; in each case, distance = 0 km corresponds to a point proximate to the Fox River mouth and distance = 120 km corresponds to a point proximate to the junction of Green Bay with the main body of Lake Michigan. Summer average TP levels (Fig. 2a) range from in excess of 100 $\mu g\ P \cdot L^{-1}$ near the Fox River mouth to less than 10 $\mu g\ P \cdot L^{-1}$ near the junction with Lake Michigan. SRP (Fig. 2a) remains detectable at the outermost station, indicating that a minimum cell quota for phosphorus may not be reached in Green Bay. TOC concentrations (Fig. 2b) range from 12 $mg \cdot L^{-1}$ in the inner bay to approximately 3 $mg \cdot L^{-1}$ in the outer bay. The particulate fraction comprises 20–30% of the total over the first 40 km of the bay; POC/TOC ratios in this range are considered indicative of eutrophic conditions (Seki 1982). Chlorophyll *a* concentrations (Fig. 2c) range from approximately 80 $\mu g \cdot L^{-1}$ in inner Green Bay to 2 $\mu g \cdot L^{-1}$ near the junction with Lake Michigan; levels of 1–2 $\mu g \cdot L^{-1}$ are considered representative of northern Lake Michigan (Rockwell et al. 1980). The summer phytoplankton community in Green Bay is dominated by green algae (*Pedi-*

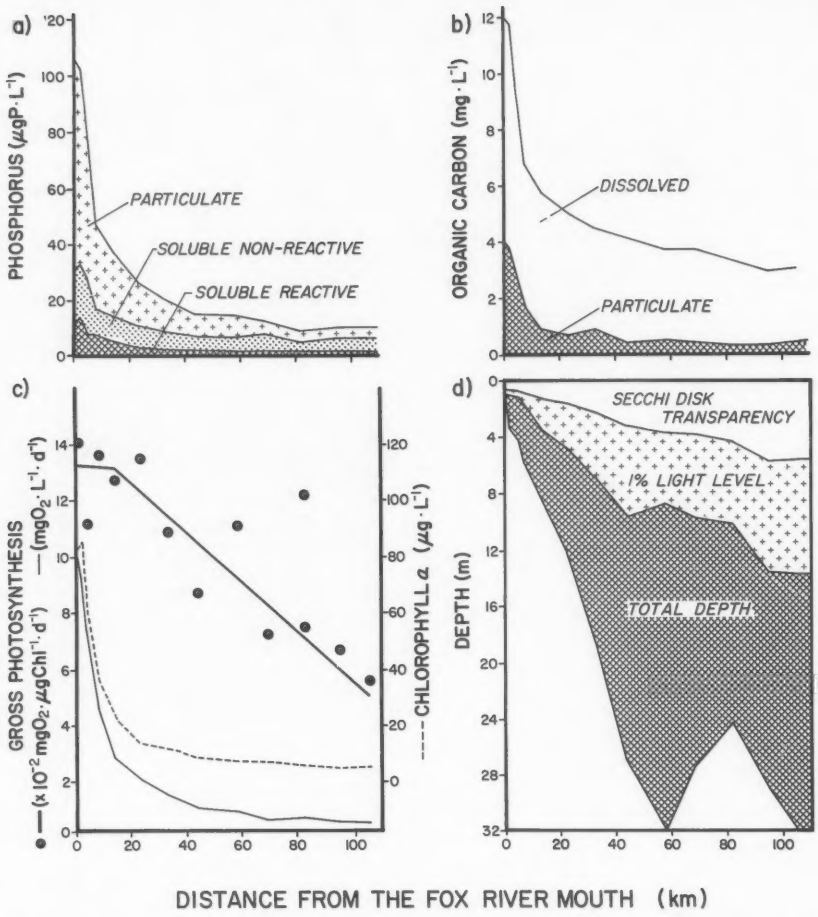


FIG. 2. Summer average spatial distribution of (a) phosphorus fractions, (b) organic carbon fractions, (c) chlorophyll *a* and gross photosynthesis, and (d) transparency and light penetration along the major (northeast–southwest) axis of Green Bay; summer average conditions, 1982.

astrum, *Staurastrum*, *Oocystis*, 22%) and diatoms (*Fragilaria*, *Melosira*, *Stephanodiscus*, 53%). A shift to blue-green algae (*Oscillatoria*, *Polycystis*, 23–73%) occurs in the inner bay in August and September, but these forms remain minor components in the mid- and outer bay regions. Summer average gross photosynthesis (measured in the laboratory, mg $O_2 \cdot g\ Chl^{-1} \cdot d^{-1}$) decreases with distance from the Fox River mouth (Fig. 2c). The form of the photosynthesis–distance profile suggests a region of near maximum growth (phosphorus saturation) over the first 20–30 km, followed by a region of submaximum growth (increasing phosphorus limitation) with distance from the Fox River mouth. Light penetration (Fig. 2d) increases with distance from the Fox River, with the 1% light level reaching nearly one half the total depth in the outer bay. The summer average Secchi disk transparency in the highly turbid, high-chlorophyll waters of the inner bay is 0.6 m, increasing to almost 6 m in the outer bay (Fig. 2d). Each of these characteristics provides an example of the strong gradient in water quality and trophic conditions which exists along the major axis of Green Bay. The gradient is permanent and stable, except near the Fox River mouth where plume migration in response to wind conditions leads to some degree of variability.

Field Verification

Our comprehensive data set, assembled for a single system, during a single season, over a wide range of nutrient and trophic conditions, offers a special opportunity for field verifying models for phosphorus and phytoplankton growth. The Droop and Monod models relate the net specific growth rate to selected measures of nutrient availability. Here, the gross specific growth rate, defined as the biomass-specific rate of gross photosynthesis (mg $O_2 \cdot$ unit biomass$^{-1} \cdot d^{-1}$), will be utilized to maintain consistency with Equation 1. Chlorophyll *a* ($\mu g \cdot L^{-1}$), POC ($mg \cdot L^{-1}$), and seston dry weight ($mg \cdot L^{-1}$) will be used as measures of phytoplankton biomass. Phosphorus availability was considered in two ways: (1) SRP and TP in the water column (external, Monod model) and (2) phosphorus stored in the cells, mass PP per mass POC (internal, Droop model).

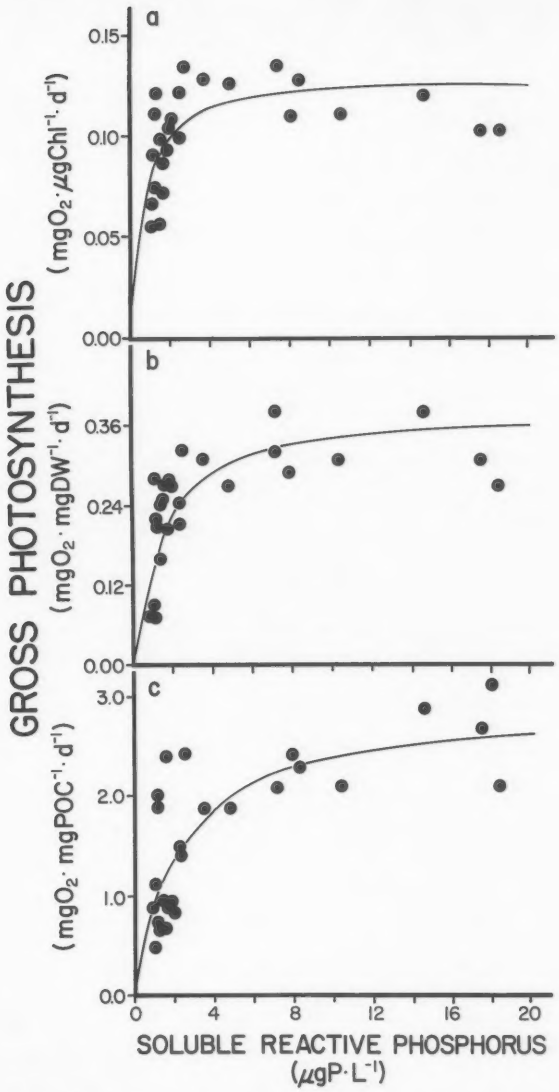


FIG. 3. Gross photosynthesis as a function of soluble reactive phosphorus concentration with biomass expressed as (a) chlorophyll *a*, (b) seston dry weight, and (c) particulate organic carbon; Green Bay, summer average conditions, 1982.

The stability of the water quality gradient along the major axis of Green Bay permits the use of summer average values for the model verification process. Nutrient and biomass data were averaged for the entire study period (summer average) at each station; data sets from single cruises were similar in form, but contained more scatter. Figures 3a–3c are plots of the summer average gross photosynthetic rate versus summer average SRP concentration, with photosynthesis normalized per unit chlorophyll *a*, dry weight seston, and POC, respectively. The fit of these data to the Monod model are best for chlorophyll *a* (CV = 19.1%), the most direct measure of photosynthesizing phytoplankton biomass of those considered. The next best fit (CV = 23.7%) is obtained for dry weight seston; apparently

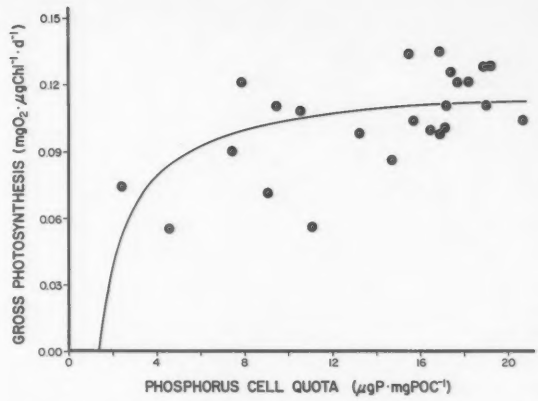


FIG. 4. Gross photosynthesis per unit chlorophyll *a* as a function of phosphorus cell quota; Green Bay, summer average conditions, 1982.

aberrant points at high phosphorus levels represent stations in the inner bay where a substantial fraction of the seston is tripton (detritus or terrigenous in origin) and not representative of the living phytoplankton community. The poorest fit to the Monod model is for POC (CV = 30.9%); the quality of the POC data is impacted by the lack of sensitivity in determining POC by difference (TOC − DOC) when the particulate fraction is small. Concentration by filtration and analysis by filter combustion/IR gas analysis would have yielded better data. The fit of field data to the model output presented in Fig. 3 represents field verification of the Monod model relating substrate (SRP) and phytoplankton growth. Values for kinetic coefficients (e.g. K_s) are presented later and are discussed in relation to critical phosphorus levels for phytoplankton growth.

Expansion of this analysis to the Droop model requires an expression of the cell quota, i.e. mass of PP per unit biomass. Two of the parameters used as biomass estimates for calculation of the specific rate of photosynthesis (chlorophyll *a* and seston dry weight) proved unsuitable for calculating cell quota. Chlorophyll *a* provides excellent normalization of photosynthetic rate, but fails for calculation of cell quota because the cellular chlorophyll *a* content varies with ambient light conditions. Thus, high phosphorus/low light (high chlorophyll *a*) conditions yield similar cell quotas to low phosphorus/high light (low chlorophyll *a*) situations. Seston dry weight, as a parameter for calculation of cell quota, again suffers due to the presence of a nonliving particulate matter component. The best biomass parameter for calculating phosphorus cell quota is POC. The relationship between chlorophyll-specific gross photosynthesis and phosphorus cell quota as predicted by the Droop model is illustrated in Fig. 4. No data are available from Green Bay for the region near Q_0, the minimum cell quota. It is unlikely that populations even exist in the natural environment (suboptimal light and temperature) in close proximity to the minimum cell quota, which, by definition, is where growth ceases. In Green Bay, where phosphorus levels remain well above the limit of detection, it is especially unlikely that internal pools ever approach the minimum cell quota. It would be valuable to extend the work presented here to highly oligotrophic waters such as Lake Superior to provide additional verification at low cell quotas. At the opposite end of the range, it is also doubtful that highly saturated internal pools will be observed in the Green Bay system. Maximum internal pool

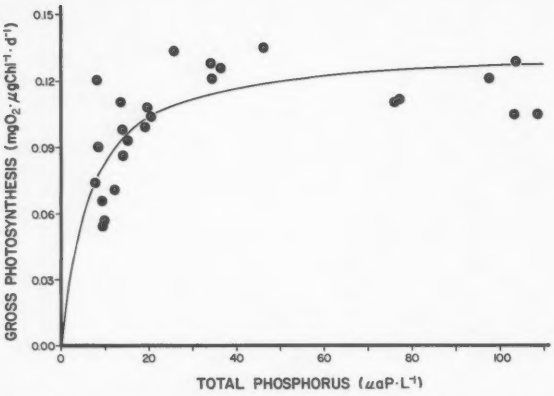


FIG. 5. Gross photosynthesis per unit chlorophyll *a* as a function of total phosphorus concentration; Green Bay, summer average conditions, 1982.

saturation is associated with extremely high SRP levels (e.g. >100 μg $P \cdot L^{-1}$) (Auer and Canale 1982; Tilman and Kilham 1976), much higher than those observed in the open waters and embayments of the Great Lakes. Despite the limited range in cell quota values, field data for Green Bay provide a good fit to the Droop model (CV = 21.2%).

The Monod and Droop models have been verified in their application for modeling growth by field populations of phytoplankton. The most common application for such models is in quantifying the relationship between phosphorus loading and water quality characteristics associated with phytoplankton growth. Phosphorus management strategies are traditionally based on the TP content of the water. It is necessary therefore to consider physiological models for phosphorus and phytoplankton growth from a total phosphorus viewpoint. TP includes three components: (1) SRP, the form thought most likely to represent phosphorus directly available for algal growth, (2) soluble nonreactive phosphorus, largely organic and at least partially available for algal growth through enzymatic hydrolysis, and (3) PP, stored in living cells, present in organic detritus, and adsorbed to abiotic particulate surfaces. When the detrital and abiotic fractions are small, the quantity TP represents the sum of the external and internal phosphorus reserves of the system. Figure 5 is a plot of summer average TP in Green Bay versus the chlorophyll-specific gross photosynthetic rate; the fit of a Monod-type function to these data is better than that obtained for SRP (CV = 18.2%). We suggest that a total phosphorus approach to lake management is consistent not only with applied interests, but with physiological and mechanistic considerations as well.

Identification of Critical Phosphorus Levels

Field verification of the Monod and Droop models can be used to test the credibility of existing estimates of critical phosphorus levels relating to the eutrophication process. Empirical relationships have been developed to predict water quality characteristics (e.g. chlorophyll *a*, Secchi disk transparency) as a function of phosphorus concentration (Dillon and Rigler 1974, 1975; Riley and Prepas 1985). The relationships have been extended to identify TP boundary values for trophic categories (Chapra and Dobson 1981; Vollenweider 1982). Despite their statistical quality and widespread application, the basis for applying empirical models for trophic state determination remains subjective and thus leads to a certain degree of uncertainty. Phosphorus boundary values for trophic categories may be established based on a knowledge of phytoplankton nutrient physiology (the Droop and Monod models), thus linking the empirical models mechanistically to the metabolism of the lake.

Critical Phosphorus Levels and Growth Rate

An improved model fit to the data for chlorophyll-specific gross photosynthesis as a function of phosphorus concentration would be achieved with a nonzero intercept on the *x*-axis (see Fig. 3 and 5), i.e. growth does not begin until a threshold phosphorus concentration is reached. The nonzero *x*-intercept may indicate that (1) a minimum phosphorus concentration utilizable by the phytoplankton (e.g. the threshold concentration of Caperon and Meyer 1972) exists, (2) a portion of the phosphorus is chemically unavailable for phytoplankton growth (see DePinto et al. 1981), or (3) a portion of the measured SRP is an artifact of the chemical analysis (see Tarapchak et al. 1982a, 1982b). In any case, the presence of a nonzero *x*-intercept is inconsistent with the assumption of the Monod model that all substrate is available.

The Monod function may be modified to accommodate this observation by defining a threshold phosphorus concentration for growth to begin and equating that value to that of the nonzero intercept:

$$(5) \quad PG = PG_{max} \cdot \left[\frac{(P - P_{t,\mu})}{((K_s - P_{t,\mu}) + (P - P_{t,\mu}))} \right]$$

where PG = chlorophyll-specific gross photosynthetic rate (mg $O_2 \cdot \mu g\ Chl^{-1} \cdot d^{-1}$), PG_{max} = maximum chlorophyll-specific gross photosynthetic rate (mg $O_2 \cdot \mu g\ Chl^{-1} \cdot d^{-1}$), P = SRP or TP (μg $P \cdot L^{-1}$), $P_{t,\mu}$ = threshold phosphorus concentration for commencement of growth (μg $P \cdot L^{-1}$), and K_s = Monod-type half-saturation constant for chlorophyll-specific gross photosynthesis (μg $P \cdot L^{-1}$). Values for the maximum chlorophyll-specific gross photosynthetic rate and the half-saturation constant were estimated statistically: $PG_{max} = 0.133 \pm 0.009$ mg $O_2 \cdot \mu g\ Chl^{-1} \cdot d^{-1}$, $K_s = 0.91 \pm 0.21$ μg $P \cdot L^{-1}$ as SRP, and $K_s = 8.5 \pm 1.1$ μg $P \cdot L^{-1}$ as TP. The fit of the function presented as Equation 5 is compared with data for Green Bay in Fig. 6a and 6b; model fit is quite good: CV = 18.8 and 16.2% for SRP and TP, respectively. The threshold phosphorus concentrations for growth were estimated statistically at 0.5 ± 0.4 μg $P \cdot L^{-1}$ for SRP and 4.3 ± 2.8 μg $P \cdot L^{-1}$ for TP.

Phosphorus concentrations corresponding to the boundary conditions for various trophic state categories may be identified from Fig. 6a and 6b. Mechanistically, it is satisfying to consider oligotrophy as that region on the modified Monod curve where growth rate increases linearly with the phosphorus concentration, ultraoligotrophy being the region at and below the threshold phosphorus concentration. Eutrophy is defined as the saturated region on the curve, where growth is unresponsive to changes in phosphorus concentration. The transitional region between oligotrophic and eutrophic conditions is considered representative of mesotrophy. Figure 7a illustrates the graphical technique used to assign phosphorus concentrations as boundary conditions for each trophic state category. Boundary condition phosphorus concentrations derived by this method from the function presented as Equation 5 and coefficients

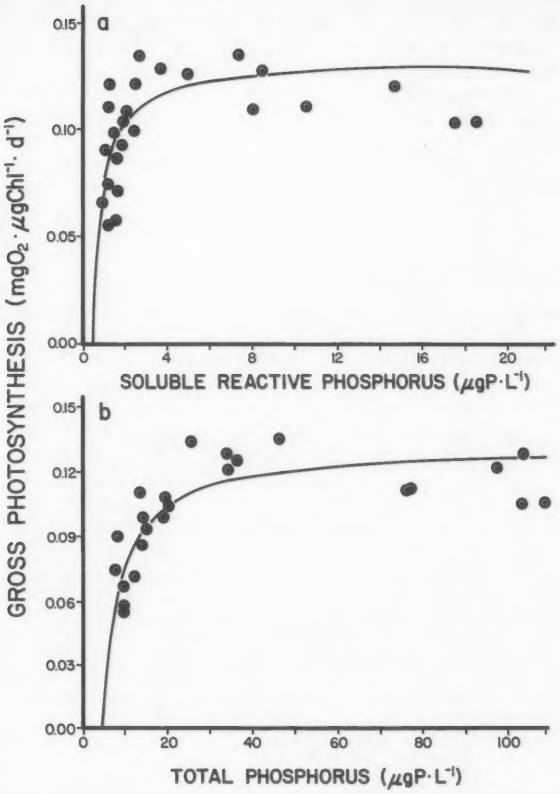

a
b
GROSS PHOTOSYNTHESIS ($mgO_2 \cdot \mu gChl^{-1} \cdot d^{-1}$)
SOLUBLE REACTIVE PHOSPHORUS ($\mu gP \cdot L^{-1}$)
TOTAL PHOSPHORUS ($\mu gP \cdot L^{-1}$)

FIG. 6. Gross photosynthesis per unit chlorophyll *a* as a function of (a) soluble reactive phosphorus concentration and (b) total phosphorus concentration, adjusted in consideration of threshold substrate levels (Equation 5).

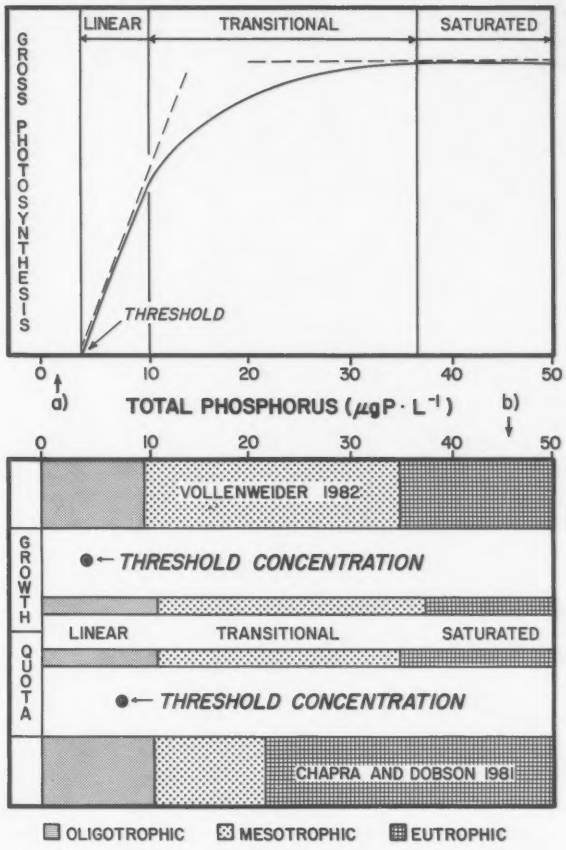


FIG. 7. Phosphorus concentrations corresponding to the bounds for trophic state categories: (a) method utilized for boundary concentration identification and (b) comparison of boundary concentrations with published estimates.

estimated statistically from Fig. 6a and 6b are as follows:

	Phosphorus form	
Trophic state category	SRP ($\mu g\ P \cdot L^{-1}$)	TP ($\mu g\ P \cdot L^{-1}$)
Ultraoligotrophic	<0.5	<4.3
Oligotrophic	0.5–1.2	4.3–11.5
Mesotrophic	1.2–8.0	11.5–37.5
Eutrophic	>8.0	>37.5

These are compared with similar published estimates for total phosphorus in Fig. 7b.

Vollenweider (1982, p. 75) established fixed boundaries for trophic state categories in the OECD lakes based upon "best judgement as to the transition between two neighboring categories." Chapra and Dobson (1981) set similar boundaries for the Laurentian Great Lakes by specifying the limits of mesotrophy on the basis of Secchi disk transparency (3–5 m) and calculating corresponding phosphorus levels from a regression equation. Trophic state boundary condition values based on the modified Monod model using data from Green Bay compare well with these published values, despite the subjective nature of the empirical approach used for the OECD lakes and the Laurentian Great Lakes. The most significant difference lies with the upper limit for mesotrophy set by Chapra and Dobson (1981) at 21.7 $\mu g\ P \cdot L^{-1}$, TP, and by the current study and Vollenweider (1982) at approximately 35 $\mu g\ P \cdot L^{-1}$, TP. This variation corresponds to a difference of 3.0 m (Chapra and Dobson 1981) versus 1.9 m (this study; Vollenweider 1982) for Secchi disk transparency as the upper bound for mesotrophy. The results presented here permit interpretation of trophic state relationships based on phytoplankton physiology and water column phosphorus concentration. Additional insight may be gained by considering similar relationships for phytoplankton physiology and internal phosphorus or cell quota.

Critical Phosphorus Levels and Cell Quota

Internal phosphorus or cell quota levels are a reflection of the cell's external nutrient environment. Low internal phosphorus levels and slow growth rates are associated with phosphorus-poor environments whereas high internal phosphorus levels and near-maximum growth rates are observed at high phosphorus concentrations. The change in size of the internal phosphorus pool over a range of phosphorus values may be indicative of the metabolic condition of the phytoplankton and the overall

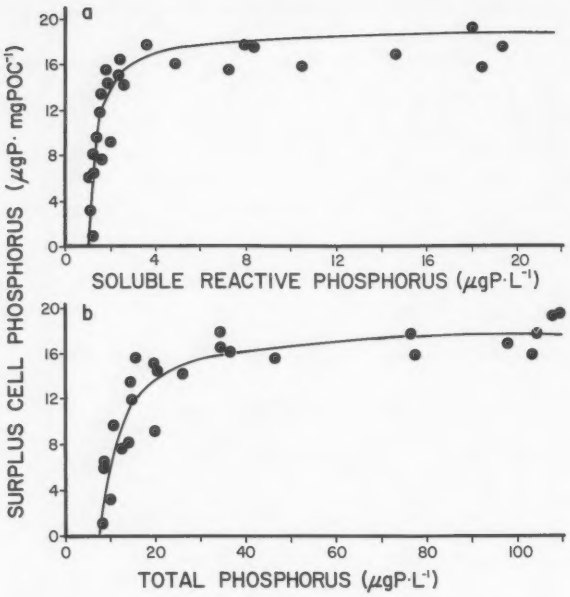


FIG. 8. Surplus cell phosphorus as a function of (a) soluble reactive phosphorus concentration and (b) total phosphorus concentration; Green Bay, summer average conditions, 1982.

trophic state of the system.

To test this hypothesis, plots of surplus cell quota versus SRP and TP concentration (Fig. 8) were prepared using Equation 5, modified for use with cell quota data:

$$(6) \quad Q_s = Q_{s,\max} \cdot \left[\frac{(P - P_{t,Q})}{((k_Q - P_{t,Q}) + (P - P_{t,Q}))} \right]$$

where Q_s = surplus cell quota (μg PP·mg POC^{-1}, $Q_{s,\max}$ = maximum surplus cell quota (μg PP·mg POC^{-1}), P = SRP or TP (μg $P \cdot L^{-1}$), $P_{t,Q}$ = critical phosphorus concentration for accumulation of surplus cell quota (μg $P \cdot L^{-1}$), and k_Q = half-saturation constant for accumulation of surplus cell quota (μg $P \cdot L^{-1}$). Surplus cell quota (Q_s) is defined as the cell quota present in excess of the minimum cell quota ($Q - Q_0$); the minimum cell quota was set at 1.4 μg PP·mg POC^{-1} as determined by statistical analysis of the data presented in Fig. 4. Surplus cell quota may be considered conceptually analagous to the boiling water extractable phosphorus of Fitzgerald and Nelson (1966).

Values for the maximum surplus cell quota and the half-saturation constant were estimated statistically: $Q_{s,\max} = 18.5 \pm 0.9$ μg PP·mg POC^{-1}, $k_Q = 1.36 \pm 0.08$ μg $P \cdot L^{-1}$ as SRP, and $k_Q = 11.7 \pm 1.0$ μg $P \cdot L^{-1}$ as TP. The fit of the Green Bay field data to the surplus cell quota function presented as Equation 6 is quite good: CV = 17.1 and 16.3% for SRP and TP, respectively. The threshold phosphorus concentrations for accumulation of surplus cell quota were 1.01 ± 0.06 μg $P \cdot L^{-1}$ as SRP and 7.2 ± 0.6 μg $P \cdot L^{-1}$ as TP. Boundary values for trophic categories established in the previous section using growth rate data may be examined here in a similar fashion in terms of cell quota. The threshold TP level for accumulation of surplus cell quota ($P_{t,Q}$), the region of linear increase in Q_s with TP, and the region of saturation in Q_s with respect to TP are identified in Fig. 7b. Phosphorus concentrations corresponding to trophic state boundaries established using surplus cell quota data are quite similar to those identified using growth rate information; again, these boundaries correspond well to empirically derived estimates (e.g. Chapra and Dobson 1981; Vollenweider 1982).

The mechanistic criteria used here to identify phosphorus concentrations corresponding to bounds for trophic state categories may be shown to be conceptually consistent with empiricial models relating phosphorus, chlorophyll *a*, and transparency. The linear form of the empirical phosphorus–chlorophyll (Reckhow and Chapra 1983) and chlorophyll–transparency (Dillon and Rigler 1975) functions at low phosphorus concentrations corresponds to the linear form of the growth rate and surplus cell quota relationships shown in Fig. 6 and 8. Over this oligotrophic range, the phytoplankton remain strongly phosphorus limited, and growth, surplus cell quota, standing crop (chlorophyll), and transparency are highly sensitive to changes in phosphorus concentration. Under high phosphorus (eutrophic) conditions, the phytoplankton become phosphorus saturated, and growth rate, standing crop, and surplus cell quota no longer respond to increases in phosphorus concentration. The form of the empirical function for phosphorus and chlorophyll is one of continued increase over the eutrophic region because the chlorophyll/biomass stoichiometry of the cells has changed in response to the reduced light levels characteristic of high standing crop environments (Falkowski 1980). The shape of the empirical relationship observed for chlorophyll and transparency flattens out in the eutrophic region because, although the chlorophyll/biomass ratio increases (shade adaptation), the phytoplankton standing crop remains relatively constant. We conclude from this comparison of the mechanistic and empirical functions that both approaches have a strong basis in phytoplankton nutrient physiology.

Applications for Water Quality Management

Our field verification of the Droop and Monod models and the expression of that verification in terms of TP may be applied in several ways to the analysis of phosphorus limitation and phytoplankton dynamics in lakes. The verification provides a mechanistic explanation for simple and direct empirical correlations between TP and other water quality variables such as transparency and chlorophyll *a*, and potentially for more complex phenomena such as hypolimnetic oxygen depletion and sediment oxygen demand. Correlations such as this have been proposed for inclusion in basinwide management scenarios regionally (Great Lakes, Chapra 1980a) and worldwide (OECD lakes, Vollenweider 1982). Field verification of physiological models for phosphorus and phytoplankton growth and subsequent mechanistic interpretation of empirical correlations establishes the model credibility required for successful management implementation.

Chapra and Sonzogni (1979) used a mass balance approach to compute a TP budget for the Great Lakes. The model may be used to calculate the impact of reduced TP loads on lakewide TP levels. The modified Monod function may be applied in conjunction with such mass balance models to establish the current trophic condition of lakes as well as their sensitivity to change in phosphorus concentration. As an example, Figure 9 identifies the position of various Great Lakes' basins on the

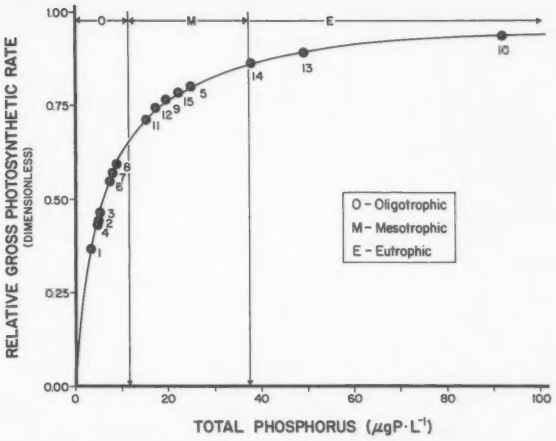


FIG. 9. Trophic state of selected basins in the Great Lakes based on the gross photosynthesis – total phosphorus model presented as Equation 5. Input data for total phosphorus are as follows: (1) Lake Superior, 3.6 (Weiler 1978); (2) central Lake Huron, 4.8 (IJC 1977); (3) southern Lake Huron, 5.3 (IJC 1977); (4) Georgian Bay, 4.7 (IJC 1977); (5) Saginaw Bay, 25.0 (IJC 1977); (6) northern Lake Michigan, 7.4 (Rockwell et al. 1980); (7) southern Lake Michigan, 8.0 (Rockwell et al. 1980); (8) northern Green Bay, 8.9 (this study); (9) mid Green Bay, 19.6 (this study); (10) southern Green Bay, 92.0 (this study); (11) eastern Lake Erie, 15.5 (Dobson et al. 1974); (12) central Lake Erie, 17.8 (Dobson et al. 1974); (13) western Lake Erie, 49.4 (Dobson et al. 1974); (14) nearshore Lake Ontario, 38.0 (OME 1980); (15) offshore Lake Ontario, 22.0 (Chapra 1980b).

gross photosynthesis – TP plot originally presented as Fig. 6b. Gross photosynthesis is expressed as a dimensionless relative rate by rearrangement of Equation 5 (relative rate = PG/PG_{max}). According to this scheme, Lakes Superior, Huron, and Michigan and northern Green Bay and Georgian Bay are classified as oligotrophic, Saginaw Bay, middle Green Bay, the east and central basins of Lake Erie, and offshore Lake Ontario as mesotrophic, and western Lake Erie, nearshore Lake Ontario, and southern Green Bay as eutrophic. By their proximity to the oligotrophic–mesotrophic boundary, Lake Michigan and the central and eastern basins of Lake Erie hold the greatest promise for change, albeit in different directions. The nearshore waters of Lake Ontario, the western basin of Lake Erie, and southern Green Bay are saturated with respect to phosphorus and would not show a dramatic response to incremental changes in TP concentration.

A more comprehensive management tool may be created by combining a mass balance model for phosphorus, the modified Monod function for predicting trophic state, and empirical functions relating phosphorus concentration to other water quality conditions (e.g. transparency, chlorophyll levels, and dissolved oxygen depletion). Heidtke et al. (1985) demonstrated the application of this management approach for screening the impact of land use management practices on water quality in Green Bay.

Acknowledgements

This research was supported by grants from the U.S. Environmental Protection Agency, Office of Grants and Centers, Washington, D.C. (grant No. R809521), and the U.S. Environmental Protection Agency, Environmental Research Laboratory, Duluth, MN (grant No. R810076). Partial travel support and publication costs were provided by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI. We gratefully acknowledge the efforts of Larry Londo and the crew of the R/V *SISU* in sample collection and processing. F. J. Hibbler of the Academic Computer Services at Michigan Technological University graciously provided assistance with statistical analyses. The manuscript profited from detailed critical reviews by S. W. Effler and G-Y. Rhee.

References

AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1980. Standard methods for the examination of water and wastewater. 15th ed. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, DC. 1134 p.

AUER, M. T., AND R. P. CANALE. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 3. The dependence of growth rates on internal phosphorus pool size. J. Great Lakes Res. 8: 93–99.

BIERMAN, V. J. JR., AND D. M. DOLAN. 1981. Modeling of phytoplankton–nutrient dynamics in Saginaw Bay, Lake Huron. J. Great Lakes Res. 7: 409–439.

BURNISON, B. K. 1980. Modified dimethyl sulfoxide (DMSO) extraction for chlorophyll analysis of phytoplankton. Can. J. Fish. Aquat. Sci. 37: 729–733.

CAPERON, J., AND J. MEYER. 1972. Nitrogen-limited growth of marine phytoplankton — II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. Deep-Sea Res. 19: 619–632.

CHAPRA, S. C. 1980a. Application of the loading concept to the Great Lakes, p. 135–152. *In* R. C. Loehr, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for the Great Lakes. Ann Arbor Science Publishers, Ann Arbor, MI.

1980b. Simulation of recent and projected total phosphorus trends in Lake Ontario. J. Great Lakes Res. 6: 101–112.

CHAPRA, S. C., AND H. F. H. DOBSON. 1981. Quantification of the lake typologies of Naumann (surface quality) and Thienemann (oxygen) with special reference to the Great Lakes. J. Great Lakes Res. 7: 182–193.

CHAPRA, S. C., AND W. C. SONZOGNI. 1979. Great Lakes total phosphorus budget for the mid-1970's. J. Water Pollut. Control Fed. 51: 2524–2533.

DEPINTO, J. V., T. C. YOUNG, AND S. C. MARTIN. 1981. Algal-available phosphorus in suspended sediments from lower Great Lakes tributaries. J. Great Lakes Res. 7: 299–310.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

DITORO, D. M. 1980. Applicability of cellular equilibrium and Monod theory to phytoplankton growth kinetics. Ecol. Model. 8: 201–218.

DITORO, D. M., AND J. P. CONNOLLY. 1980. Mathematical models of water quality in large lakes. Part 2. Lake Erie. U.S. Environmental Protection Agency, Duluth, MN. 231 p.

DOBSON, H. F. H., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron, and Superior. J. Fish. Res. Board Can. 31: 731–738.

DROOP, M. R. 1968. Vitamin B_{12} and marine ecology. IV. The kinetics of growth, uptake, and inhibition in *Monochrysis lutheri*. J. Mar. Biol. Assoc. U.K. 48: 629–636.

FALKOWSKI, P. G. 1980. Light–shade adaptation in marine phytoplankton, p. 99–119. *In* P. G. Falkowski [ed.] Primary productivity in the sea. Plenum Press, New York, NY.

FITZGERALD, G. P., AND T. C. NELSON. 1966. Extractive and enzymatic analyses for limiting or surplus phosphorus in algae. J. Phycol. 2(1): 32–37.

HEIDTKE, T. M., M. T. AUER, R. P. CANALE, AND T. A. D. SLAWECKI. 1985. Coupling nonpoint pollution and water quality models: an example for the Green Bay – Fox River watershed. Proceedings of the Non-point Pollution Abatement Symposium, Marquette University, Milwaukee, Wisconsin, April 1985. 12 p.

INTERNATIONAL JOINT COMMISSION (IJC). 1977. The waters of Lake Huron and Lake Superior. Volume II. Lake Huron. Upper Lakes Reference Group, Windsor, Ont. 448 p.

JANNASCH, H. W. 1974. Steady state and the chemostat in ecology. Limnol. Oceanogr. 19: 716–720.

LIND, O. T. 1979. Handbook of common methods in limnology. C. V. Mosby Company, St. Louis, MO. 154 p.

MONOD, J. 1942. Recherches sur la croissance des cultures bactériennes. Hermann, Paris. 210 p.

MORTIMER, C. H. 1978. Water movement, mixing and transport in Green Bay, p. 10–56. *In* H. J. Harris and V. Garsow [ed.] Green Bay Workshop Proceedings, University of Wisconsin Sea Grant Publ. No. WIS-SG-78-234, Madison, WI.

ONTARIO MINISTRY OF THE ENVIRONMENT (OME). 1980. Lake Ontario nearshore water quality atlas, 1976–1979. Water Resources Branch, Great Lakes Unit, Toronto, Ont. 88 p.

RALSTON, M. 1983. PAR, Derivitive-free nonlinear regression, p. 305–314. In W. J. Dixon [ed.] BMDP statistical software. University of California Press, Berkeley, CA.

RECKHOW, K. H., AND S. C. CHAPRA 1983. Engineering approaches for lake management. Volume 1. Data analysis and empirical modeling. Butterworth Publishers, Boston, MA. 340 p.

RILEY, E. T., AND E. E. PREPAS. 1985. Comparison of the phosphorus–chlorophyll relationships in mixed and stratified lakes. Can. J. Fish. Aquat. Sci. 42: 831–835.

ROCKWELL, D. C., D. S. DEVAULT, M. F. PALMER, C. V. MARION, AND R. J. BOWDEN. 1980. Lake Michigan intensive survey: 1976–1977. U.S. Environmental Protection Agency, Chicago, IL. 155 p.

ROZNOWSKI, D. M., AND M. T. AUER. 1984. Tributary loadings to Green Bay: a mass balance approach. U.S. Environmental Protection Agency, Duluth, MN. 74 p.

SAGER, P. E., AND J. H. WIERSMA. 1972. Nutrient discharges to Green Bay, Lake Michigan from the lower Fox River, p. 132–148. *In* Proc. 15th Conf. Great Lakes Res., International Association for Great Lakes Research, Toronto, Ont.

SEKI, H. 1982. Organic materials in aquatic ecosystems. CRC Press, Inc., Boca Raton, FL. 201 p.

SENFT, H. W. 1978. Dependence of light-saturated rates of algal photosynthesis on intracellular concentrations of phosphorus. Limnol. Oceanogr. 23: 709–718.

SONZOGNI, W. C., T. J. MONTEITH, W. N. BACH, AND V. G. HUGHES. 1978. United States Great Lakes tributary loads. International Joint Commission, Windsor, Ont. 187 p.

TARAPCHAK, S. J., S. M. BIGELOW, AND C. RUBITSCHUN. 1982a. Overestimation of orthophosphate concentrations in surface waters of southern Lake Michigan: effects of acid and ammonium molybdate. Can. J. Fish. Aquat. Sci. 39: 296–304.

1982b. Soluble reactive phosphorus measurements in Lake Michigan: filtration artifacts. J. Great Lakes Res. 8: 550–557.

TILMAN, D., AND S. S. KILHAM. 1976. Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semicontinuous culture. J. Phycol. 12: 375–383.

VOLLENWEIDER, R. A. 1969. A manual on methods for measuring primary production in aquatic environments. Int. Biol. Prog. Handb. 12. Blackwell Scientific Publications, Oxford. 213 p.

VOLLENWEIDER, R. A. [ED.] 1982. Eutrophication of waters: monitoring, assessment and control. Organization Economic Cooperation and Development, Paris, France. 154 p.

WEILER, R. R. 1978. Chemistry of Lake Superior. J. Great Lakes Res. 4: 370–385.

Nutrient Status of Phytoplankton Blooms in Norwegian Waters and Algal Strategies for Nutrient Competition[1,2]

Egil Sakshaug

The Biological Station, University of Trondheim, The Museum, N-7000 Trondheim, Norway

and Yngvar Olsen

Institute of Marine Biochemistry, University of Trondheim, N-7034 Trondheim, Norway

Sakshaug, E., and Y. Olsen. 1986. Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition. Can. J. Fish. Aquat. Sci. 43: 389–396.

During blooms in Norwegian waters phytoplankton communities are phosphorus limited in fresh and brackish waters, and balanced or even nitrogen limited in high-salinity marine waters. This results from the high N/P ratio for available nutrients before onset of blooms in freshwater relative to seawater (N/P (atoms) >100 and 12–16, respectively). Algal N/P ratios at nutrient saturation vary between 8 and 27 among species, and average 16. A low ratio at nutrient saturation may imply P limitation even in high-salinity waters (e.g. *Skeletonema costatum*). In general, nutrient deficiency becomes more pronounced as the biomass increases. Addition of sewage shifts natural systems toward N limitation, which may therefore be a secondary effect of accelerated eutrophication. Interspecific competition in nutrient-limited communities depends on the nutrient requirement of individual species and the mode of nutrient uptake. In our example the desmid *Staurastrum luetkemuellerii* outcompetes the cyanobacterium *Microcystis aeruginosa* in a chemostat when the nutrient supply is continuous; the opposite happens when nutrient supply is pulsed.

Dans les eaux norvégiennes, les efflorescences phytoplanctoniques sont limitées par la quantité de phosphore dans les eaux douces et saumâtres, et par l'azote dans les eaux marines à salinité élevée où un équilibre peut aussi exister. Ceci est le résultat du rapport N/P élevé dans les bioéléments disponibles avant le début des efflorescences en eau douce par rapport au milieu marin (nombre d'atomes N/P > 100 ou 12–16, respectivement). Les rapports N/P dans les algues au niveau de saturation en bioéléments ont varié de 8 à 27 parmi les espèces (moyenne : 16). Un faible rapport à ce niveau peut signifier une concentration limitative de P, même dans des eaux à salinité élevée (p. ex. *Skeletonema costatum*). En général, la carence nutritive devient plus prononcée à mesure que la biomasse augmente. L'apport d'eaux usées entraîne une restriction azotique des écosystèmes naturels qui peut être un effet secondaire d'une eutrophisation accélérée. Dans les communautés limitées par la présence de bioéléments, la compétition interspécifique dépend des besoins en bioéléments, la compétition interspécifique dépend des besoins en bioéléments de chaque espèce et du mode de captation. Dans l'exemple présenté, la desmidiale *Staurastrum luetkemuellierii* l'a emporté sur la cyanobactérie *Microcystis aeruginosa* dans un chemostat où l'apport de bioéléments était continu; le contraire s'est produit quand cet apport était rythmique.

Received November 19, 1984
Accepted April 19, 1985
(J8020)

Reçu le 19 novembre 1984
Accepté le 19 avril 1985

Phytoplankton blooms are temporary phenomena and occur primarily in coastal zones, in landlocked areas, fjords, and lakes. A marked spring bloom is also typical for the open ocean at medium and high latitudes. In general, the nutrient supply limits growth at the end of a bloom, with the probable exception of blooms in the Antarctic Ocean (Sakshaug and Holm-Hansen 1984).

Here we summarize our studies of phytoplankton blooms in various Norwegian waters, extending from oceanic waters via fjords to lakes. These studies have been carried out since 1970. Some data have been presented elsewhere (Haug et al. 1973; Jensen and Sakshaug 1973; Sakshaug and Myklestad 1973; Sakshaug 1978; Sakshaug et al. 1981; Olsen et al. 1981; Sakshaug et al. 1983, Olsen et al. 1983a), but synthesis of results has not been presented before.

Our studies on phytoplankton have dealt with the chemical composition of the populations from the fundamental view that algae rather than the environment provide the most direct and relevant answers regarding algal behaviour. These studies have yielded interesting information on algal bloom dynamics. By comparing these results with laboratory data, it is possible to generalize our results (Myklestad 1977; Sakshaug 1977a; Sakshaug and Holm-Hansen 1977; Hegseth and Sakshaug 1983; Olsen et al. 1983a).

When communities are multispecific, knowledge that can be derived from measurements of the average chemical composition is limited, because properties at the species level are unknown. This is unfortunate because information on nutrient

[1]This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

[2]Contribution No. 232, The Biological Station, Trondheim.

TABLE 1. Variations in the N/C ratio in a community consisting of N-saturated populations of *Staurastrum luetkemuellerii* and *Anabaena flos-aquae*. The relative biomass proportions are based on carbon (derived from plasma volume calculations). The expected N/C ratio of the mixture is compared with the results for natural blooms in P-limited Lake Haugatjønna.

% of biomass		N/C		
Staurastrum	*Anabaena*	expected	N/C natural bloom	*n*
0	100	0.25	—	—
30	70	0.19	0.16±0.03	7
49	51	0.16	0.14±0.01	4
77	23	0.10	0.10±0.03	3
100	0	0.059	—	—

competition between species and species succession is paramount in phytoplankton ecology (Tilman et al. 1982). Nonetheless, such information can be derived from autecological studies and laboratory competition studies. We have undertaken such studies and summarize them here.

The data for natural phytoplankton communities have been corrected for detrital and heterotrophic interference according to procedures described earlier (Sakshaug 1978; Olsen et al. 1983a).

Chemical Composition as Indicator of Nutrient Status

Numerous laboratory studies have shown that nutrient deficiency alters the chemical composition of algae in a relatively predictable way. Typically, the cellular fraction of the limiting nutrient is lowered per unit biomass. This ratio can be related to the growth rate by a rectangular hyperbola (Droop 1974; Paasche 1973; Rhee 1973; Olsen et al. 1983a, 1983b).

Correspondingly, when the chemical composition of a natural population is known, we may have information on whether the growth rate is reduced or not, and by which limiting nutrient. Prediction of the absolute growth rate will, however, necessitate information on the impact on the growth rate of each of the species by all relevant environmental factors. Nevertheless, qualitative information can yield valuable insight into algal bloom dynamics.

Conclusions regarding natural populations may be based on relative changes in algal chemical composition during a bloom, or the results may be compared with those from well-defined laboratory cultures. A simple approach in the latter case is to use the chemical characteristics of nutrient-saturated cultures as a reference, even if species differ in their characteristics, and differences in the light regime and the temperature introduce variation in the growth rate and the chemical composition.

We have used N/C and P/C ratios as indicators of the cellular saturation level of nitrogen and phosphorus, respectively. Most species exhibit N saturation at N/C = 0.14−0.16 (atoms), but some species differ significantly. Species with thick, organic thecae have saturation levels as low as 0.06−0.07 (e.g. *Staurastrum luetkemuellerii* Donat et Ruttner, and Ceratia), whereas the cyanobacterium *Anabaena flos-aquae* f. *lemmermannii* (Richt.) Canab has a level as high as 0.25 (Sakshaug et al. 1983, 1984). The P/C ratio at P saturation is highly species specific. We have encountered P/C ratios from 0.006 (*Amphidinium carteri* Hulburt) to 0.017 (*Skeletonema costatum* (Grev.) Cleve), and N/P ratios from 8 to 27. For these species, P has been analyzed by UV oxidation; polyphosphate stores are presumably excluded and should be small in most marine diatoms (Solórzano and Strickland 1968; Sakshaug and Holm-Hansen 1977).

Interspecific variations in intracellular nutrient levels represent no problem in cases where blooms are nearly unialgal, provided that the saturation levels for the species can be deduced, but may yield misleading conclusions in some cases of oligospecific blooms. In Table 1 we present an example from Lake Haugatjønna, where a clearly P-limited system is composed of two species with different N saturation levels. A high P supply favours *Anabaena* and a low P supply favours *Staurastrum*. If the nutrient supply gradually went from high to low during a bloom, it would appear as if the population went from N saturation to N subsaturation. In reality the cells are consistently N saturated, and the lowering of the N/C ratio would be due solely to the shift in species composition.

Multispecies blooms are also affected by this type of variation, but as long as no particular species achieves predominance, a rather predictable average saturation level may be expected. Marine species we have studied in the laboratory yield an average of N/C = 0.15, P/C = 0.010, and N/P = 16 (atoms), which corresponds to the Redfield ratio for oceanic particulate matter (Redfield et al. 1963).

We assume a threshold model for nutrient deficiency of a species (Droop 1974); i.e. only one nutrient is limiting at a given instant. If more than one nutrient is at subsaturating level, the limiting one would be the one that results in the lowest growth rate. Such predictions require full knowledge of the nutrient uptake kinetics for each species. In our studies, concerning only N and P, we have instead used variations in the N/P ratio to distinguish between N and P deficiency. This is possible provided that the uptake of N and P is uncoupled and reflects the ratio of external nutrient supply. *Skeletonema costatum*, which is the focus in our studies, seems to behave in this fashion (Myklestad 1977; Sakshaug and Holm-Hansen 1977). There may, however, be exceptions (Droop 1974). In some dinoflagellates the N levels appear so coupled to the P levels at P limitation that the N/P ratio hardly changes (Sakshaug et al. 1984).

Field Observations

In Table 2 we present the range of variation (from saturation to maximum observed deficiency) in algal chemical composition in different Norwegian waters. The N/C ratio varies 2.5-fold, the P/C ratio 3.5-fold, and the N/P ratio 6-fold. The *Skeletonema* blooms in the Trondheimsfjord are virtually unialgal. It is notable that the saturation level for naturally growing *Skeletonema* (in nutrient-rich waters below the pyknocline in May) corresponds almost exactly to the saturation level found in laboratory experiments (N/C = 0.14, P/C = 0.017, N/P = 8.1). Data on two *Skeletonema* blooms have been presented. The one in April is the first spring bloom, which is based on high winter level nutrients and which develops with batch culture-like kinetics. The one in May is more continuous and is supported by the nutrient supply from high freshwater inputs combined with entrained seawater for more than 1 mo. It is, thus, a brackish water bloom. Subsaturation with P is evident for both blooms, particularly in brackish water, whereas cellular N levels decrease only slightly. The notable increase in the N/P ratio indicates that algae were becoming P deficient.

TABLE 2. Variation in chemical composition of algal blooms (from saturation to extreme nutrient deficiency). The biomass has been corrected for detrital and heterotrophic interference. The *Skeletonema* and *Emiliania* data are from the Trondheimsfjord. The eutrophic lake is Haugatjønna, situated close to the Swedish border east of Trondheim. Data for the latter are from the control bags (no enrichment) of a series of bag experiments. Data compiled from Sakshaug et al. (1983).

	S (‰)	Biomass ($\mu g\ C \cdot L^{-1}$)	Atoms N/C	Atoms P/C	Atoms N/P	No. of samples
Skeletonema (sat.)	~32	175	0.14	0.015	9.1	4
April bloom 1977	~32	355	0.12	0.0079	15	2
May bloom 1976	~19	330	0.11	0.0043	26	4
North Sea, May bloom 1981	~32	160	0.065	0.011	5.8	4
Emiliania (sat.)[a] 1977	~30	230	0.15	0.0094	16	2
Sept. maximum	~30	250	0.13	0.0072	18	2
Eutrophic lake (sat.)[b]	—	<200	0.15	0.0097	16	3
Eutrophic lake 1980	—	>400	0.16	0.0045	35	3

[a]60% *Emiliania huxleyi* by cell number.
[b]60% *Anabaena flos-aquae*, 40% *Staurastrum luetkemuellerii* by carbon.

However, the maximum level of N/P = 15 in April is not higher than the Redfield ratio, so if this bloom had been a multispecies diatom community, which is usually the case in April, it would be balanced with respect to N and P. In fact, independent tests of P deficiency such as the ATP test (measured increase in ATP 2 h after adding PO_4^{3-} to a sample; Sakshaug et al. 1983; Olsen et al. 1985) did not indicate pronounced P deficiency. In contrast, the second bloom was clearly P deficient. An N/P ratio of 26 is on the P-deficiency side for most species, and the ATP test and measurements of alkaline phosphatase activity yielded highly significant responses (Myklestad and Sakshaug 1983).

Samples from a spring bloom in the North Sea off Bergen yielded clear signs of N deficiency. The N/C ratio was well below 0.1; the P/C ratio was the one expected for a P-saturated mixed diatom community. Furthermore, a maximum of *Emiliania huxleyi* (Lohm.) Hay et Mohler in the Trondheimsfjord exhibited nutrient proportions close to the Redfield ratio. Freshwater blooms, again from Lake Haugatjønna, were clearly P deficient and yielded the highest N/P ratio we have observed, namely 35.

In summary, freshwater and low-salinity brackish water clearly yield P-deficient populations when blooms develop; high-salinity waters yield populations with Redfield characteristics, or sometimes clearly N-deficient populations (e.g. North Sea).

Skeletonema blooms in the Trondheimsfjord offer insight into the relationship between the environment and algal nutrient status (Table 3). First of all, the level of ambient N is rather high in both blooms, which is not unexpected, since *Skeletonema* "feels" the environment as being rather P limited. More notable is the significant level of ambient PO_4^{3-} ($0.08-0.19\ \mu mol \cdot L^{-1}$) even when populations are P deficient. Phosphate at low levels is, however, difficult to measure in seawater because of interferences, and we have not observed any relationship between ambient phosphate and the algal nutrient status (Sakshaug 1978). A second feature is that algal P during the May bloom varies little, befitting a bloom that is continuous. On the other hand, the biomass level may vary considerably. This implies that the extent of P deficiency is related to biomass. If the biomass is small enough, the population may be nutrient saturated. In principle, this looks like a system with a fairly constant supply of "new" nutrients, whereas the biomass may be regulated through processes such as grazing and sinking.

With no apparent relationship between nutrient status and ambient nutrients, it is fruitful to examine supply of nutrients. The May bloom is composed on a mixture of freshwater and entrained subsurface water to a variable extent reflected in a variable salinity and entrainment ratio. On average, the entrainment ratio in the outer fjord in May is 1:4 (freshwater to seawater); the resulting average salinity is 26.4‰, with a residence time for the brackish layer of 13 and a 10-m layer of brackish water. This apparently coincides well with the lower boundary of the euphotic zone in May. The average daily freshwater supply to the outer fjord is $130 \times 10^6\ m^3$ in May, and the typical nutrient content is $5.4\ \mu mol\ N \cdot L^{-1}$ and $0.027\ \mu mol\ PO_4^{3-} \cdot L^{-1}$, which yields an N/P ratio of 200. In contrast, subsurface seawater is rich in PO_4^{3-} ($0.65\ \mu mol \cdot L^{-1}$) and also fairly rich in nitrate and ammonia ($6.4\ \mu mol \cdot L^{-1}$).

The nutrient concentrations of different mixtures of fresh and seawater (assuming no consumption by algae) are presented in Table 4. The variation in P and in the N/P ratio is notable. At low salinities, P limitation is most likely.

Even if the May bloom is continuous, it may also be regarded as a batch culture when applying the Lagrangian principle of following a given intact parcel of brackish water on its way out of the fjord. We may then assume that the parcel in its initial stage is seeded by the entrained water with *Skeletonema*, and that algae will gradually convert the initial nutrient mixture into biomass. How far this proceeds depends largely on how fast biomass is removed by grazing and sinking, and on the age of the parcel. The parcel will presumably be younger close to a source of freshwater, and will, thus, have a smaller biomass and exhibit less deficiency (Table 3).

In Table 4 we have assumed P limitation of *Skeletonema* at all salinities and virtually complete conversion into biomass. Low-salinity waters imply marked P deficiency at higher biomasses. The algae may remain nutrient saturated until the biomass has reached $100-340\ \mu g\ C \cdot L^{-1}$, depending on the

entrainment ratio. They will have a P/C ratio of 0.0063 and 0.0046 (values chosen according to Table 3) when reaching 250–820 and 340–1100 μg C·L^{-1}, respectively. When comparing this with corresponding data in Table 3 (see table footnotes), it becomes clear that the calculated biomass is more than twice as high as that actually observed at corresponding P/C ratios. This discrepancy is expected. A portion of the biomass is grazed and will be converted into zooplankton; another portion may sink out of the system. What is more important here is that the N/C and N/P ratios at given P/C ratios are virtually the same for corresponding entrainment ratios (Tables 3 and 4). This indicates that nutrient status of the algae is closely related to nutrient supply rather than ambient nutrient levels.

N Limitation vs. P Limitation

The data demonstrate that freshwater is strongly P limiting. This conclusion is in accordance with numerous other studies (Healey and Hendzel 1980; Nalewajko and Lean 1980; Kilham and Kilham 1980). However, this may be altered in the presence of organic pollution and phosphate-rich rocks. On the other hand, seawater has a vast store of phosphate, so large that seawater is usually assumed to be N limiting. Our data partially verify this. When the phytoplankton biomass is large enough to become nutrient deficient, the algal N/P ratio tends to become lower than the ratio of 16 assumed for the average marine alga. However, one should bear in mind that the N deficiency we have observed has not been very pronounced, apart from the North Sea samples. We thus tend to believe that most high-salinity waters may be fairly balanced in their supply of N and P relative to the average requirements of marine algae. It is important in this context that Norwegian fjords and coastal waters are generally so deep that nutrient supply from sediments becomes negligible.

There are, of course, clear-cut cases of N deficiency in marine waters. Apart from the North Sea, Narragansett Bay is one example (Smayda 1974; Sakshaug 1977a). Others are nearshore areas off southern New England (Ryther and Dunstan 1971) and the Skagerrak and Kattegat areas (Gargas 1975; Granéli 1981). In the Baltic, clear-cut N deficiency has been observed even at salinities as low as 10‰ (Niemi 1979). All these areas are shallow and/or exposed to significant amounts of sewage.

According to the commonly used definition of a person equivalent in Scandinavia, the N/P ratio in sewage is 8.8 (12 g N and 3 g P·d^{-1}). Considering the lower solubility of some nitrogenous compounds relative to phosphorous compounds, the N/P ratio for supplied nutrients may be as low as 3–5. Sewage supply will, thus, tend to shift natural systems towards N limitation. It follows in principle that any system, even freshwater, may become N limiting if the impact from sewage supply is large enough (Schindler 1977). The amount of sewage required to cause N limitation in fresh and brackish waters may take realistic proportions if the reservoir is small and the residence time is high. Fjords and lakes will exhibit marked horizontal gradients, so nearshore areas near sewage outlets may show extreme conditions even if the water body as a whole is too large to show such effects. The brackish situation in May in the Trondheimsfjord may serve as an example. It would take more than 1.1 million person equivalents of sewage to ensure algal populations with N/P ≤ 11 (when nutrient deficient) in the outer fjord. The area surrounding the outer fjord offers less than

TABLE 3. *Skeletonema* blooms in the surface layers of the Trondheimsfjord. The April bloom follows the kinetics of batch cultures. Lowered biomass towards the end is caused by sinking. The May blooms is continuous, and characteristics have been given for different biomass densities. Ambient nitrogenous nutrients are given as the sum of nitrate (measured) and ammonia as the average amount of 0.5 μmol·L^{-1} for March–May (Sakshaug 1977b). Data compiled from Sakshaug (1978) and Sakshaug et al. (1983).

	Ambient nutrients (μmol·L^{-1})		Phytoplankton (μmol·L^{-1})		Atoms					Avg. C (μg·L^{-1})	Avg. S (‰)	No. of observations
								Phytoplankton				
	N	PO_4^{3-}	N	P	ΣN	ΣP	N/P tot.	N/C	P/C	N/P		
Early April	1.7	0.14	4.8	0.37	6.0	0.51	13	0.14	0.011	13	410	32	3
Mid-April	1.5	0.08	3.6	0.23	4.6	0.31	16	0.12	0.0080	15	360	32	2
May													
C < 250 μg·L^{-1}	1.1	0.11	2.2	0.19	2.8	0.30	11	0.15[a]	0.013[a]	12[a]	180[a]	26.5	4
250 < C < 350 μg·L^{-1}	2.4	0.14	2.8	0.16	3.7	0.30	14	0.11[b]	0.0063[b]	18[b]	305[b]	23	9
C < 350 μg·L^{-1}	0.9	0.19	3.3	0.17	3.7	0.36	12	0.089[c]	0.0046[c]	19[c]	440[c]	23	4

NOTE: Values superscripted a, b, and c correspond to values in Table 4.

TABLE 4. Brackish water formed by various proportion of freshwater and seawater. Calculations based on characteristic properties of subsurface seawater in the outer Trondheimsfjord (33‰) and of river water entering the fjord (Sakshaug and Myklestad 1973). Ambient N represents the sum of nitrate and ammonia, and ambient P is orthophosphate, no consumption assumed. For conversion to phytoplankton biomass, a *Skeletonema* bloom is assumed at three different levels of P deficiency (P/C = 0.0046, P/C = 0.0063, and saturation) and no grazing and sinking. We assumed that 0.1 μmol $P \cdot L^{-1}$ is left in the water at full conversion and at least 0.1 μmol $N \cdot L^{-1}$. N/C = 0.15 is assumed to be the maximum for this ratio.

Entrainment ratio, freshwater: seawater	S(‰)	Ambients nutrients (μmol·L^{-1})			Conversion to phytoplankton								
					P/C = 0.0046			P/C = 0.0063			P/C = 0.015 (sat.)		
		N	P	N/P	C(μg·L^{-1})	N/C	N/P	C(μg·L^{-1})	N/C	N/P	C(μg·L^{-1})	N/C	N/P
1:0	0	5.4	0.027	200	—	—	—	—	—	—	—	—	—
1:0.5	11	5.7	0.23	24	340	0.15	33	250	0.15	24	100	0.15	10
1:1	16.5	5.9	0.34	17	630	0.11	24	460	0.15	24	180	0.15	10
1:2	22	6.1	0.44	14	890	0.081[c]	18[c]	650[b]	0.11[b]	17[b]	270	0.15	10
1:4	26.4	6.2	0.53	12	1100	0.065	14	820	0.089	14	340[a]	0.15[a]	10[a]
0:1	33	6.4	0.65	9.9	—	—	—	—	—	—	—	—	—

NOTE: Values superscripted a, b, and c correspond to values in Table 3.

one quarter of that amount. Consequently, sewage effects will be localized and not measurable in the system as a whole.

The primary effect of sewage addition is accelerated eutrophication. The development towards N deficiency is secondary. When signs of N deficiency occur in water that should otherwise be P limiting, it is a sign that eutrophication rates have been significantly accelerated. If blooms become a nuisance, the logical conclusion from N deficiency would be to reduce sewage supply. A discussion of remedial actions is merely a discussion of secondary effects. If the goal is to restore the old original system, sewage supply has to be reduced whether the reservoir is fresh, brackish, or marine. In fresh and brackish waters, this implies removal of P to such an extent that the system again becomes strongly P limited. Because marine waters may be fairly balanced with N and P, removal of P should also be an adequate countermeasure of pollution in those waters. The effect of P removal may, however, be considerably delayed in shallow areas where the sediments may release phosphate.

Dynamics of Multispecies Blooms

Measurements of nutrient status on natural phytoplankton communities can be a valuable diagnostic tool in phytoplankton ecology, especially in the case of unialgal blooms. Data are also valuable from an engineering point of view because they can relate the gross features of algal blooms to environmental variation, such as sewage supply. But such measurements represent a gross oversimplification of phytoplankton ecology because they cannot, except in the case of unialgal blooms, yield data at the species level. At best, we can conclude that the average properties apply to dominant species. If communities are multispecific, some minority species may be nutrient deficient (i.e. having a lowered growth rate) even if the average nutrient status of the community indicates nutrient saturation. If the system becomes nutrient enriched, some species might become predominant because of their increased growth rate, and the total biomass would increase. If looking only at the total biomass, this would seem contradictory, i.e. the community as a whole would appear nutrient saturated ($\mu = \mu_m$), but also nutrient limited in the Liebig sense, because enrichment yielded a larger biomass. Multispecificity is essential in removing this apparent paradox. Such a scenario may be relevant for oligotrophic systems, where the average nutrient status often does indicate nutrient saturation (Goldman et al. 1979). Equally, the balance point will be species specific. One species may be N limited and another one P limited in the very same mass of water, allowing them to coexist (Tilman 1977; Rhee 1978).

Pulsed Nutrient Supply and Interspecific Competition

Natural phytoplankton populations are continuously exposed to gradients of the limiting nutrients. This may include nutrient-rich pulses of different sizes, concentrations, and life times (McCarthy and Goldman 1979; Jackson 1980; Lehman and Scavia 1982). A completely homogeneous system is unlikely in nature because all nutrients are supplied from point sources (e.g. aquatic animals, runoff, the thermocline, sediment surfaces). Algae may, apart from this, also exhaust their immediate surroundings for limiting nutrients (Pasciak and Gavis 1974).

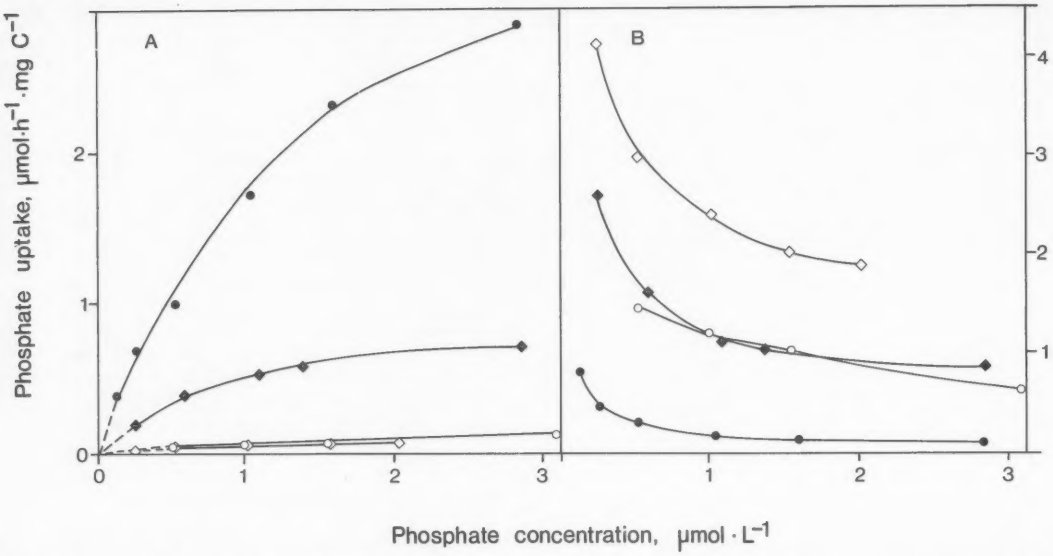


FIG. 1. Characteristics of short-term phosphate uptake in *Staurastrum leutkemuellerii* and *Microcystis aeruginosa* upon exposure to plumes of phosphate of varying concentrations. (A) Initial (0–11 min) uptake rate for P; (B) corresponding doubling times of internal P in *Staurastrum* growing at $\mu = 0.28\mu_m$ (○) and $\mu = 0.66\mu_m$ (◇) and in *Microcystis* growing at $\mu = 0.34\mu_m$ (●) and $\mu = 0.78\mu_m$ (◆). Uptake rates were measured as ^{33}P uptake in diluted (3–15 times) samples taken from steady-state continuous cultures maintained at 23°C at 90 $\mu E \cdot m^{-2} \cdot s^{-1}$ (L:D = 18:6).

We have studied species competition for P in chemostats at pulsed and continuous nutrient supply, using the desmid *Staurastrum luetkemuellerii* and the cyanobacterium *Microcystis aeruginosa* Kutz. We present here some short-term uptake experiments and some competition experiments performed with continuous cultures. The initial uptake rates (u_p) upon being exposed to pulses of phosphate are shown as a function of the phosphate concentration of the pulse in Fig. 1A. Uptake curves for both species are shown for cells growing at two different growth rates or levels of P limitation. Results reveal that *Microcystis* is more efficient in accumulating phosphate than *Staurastrum* when exposed to elevated concentrations of phosphate. Even moderately starved *Microcystis* ($\mu = 0.78\mu_m$) exhibited higher uptake rates than extremely starved *Staurastrum* ($\mu = 0.28\mu_m$). The turnover time of cellular phosphorus has been plotted as a function of the nutrient concentration in the pulse (Fig. 1B). The turnover time is given as the P/C ratio divided by the initial uptake rate (u_p). Our data show that *Microcystis* could double its cellular P content in about 5 min when starved ($\mu = 0.34\mu_m$) and when P was supplied in high concentrations (2–3 $\mu mol \cdot L^{-1}$). Extremely starved *Staurastrum* exhibited, in contrast, doubling times of its P content of 1 h. This doubling time is similar to that of moderately starved *Microcystis*.

In summary, the ability of rapid phosphate uptake was much more pronounced in *Microcystis* than in *Staurastrum*. However, both species did take up P faster when extremely starved than when moderately starved. This is in accordance with other reports (Gotham and Rhee 1981a, 1981b; Goldman and Glibert 1982).

Our experiments predict that *Microcystis* should outcompete *Staurastrum* in mixed P-limited continuous cultures if phosphate is supplied in pulses. Utilization of P for growth ($P/C \cdot \mu$) was less efficient in *Microcystis* than in *Staurastrum*, but this was compensated by the more rapid uptake of P by the former species (cf. Fig. 1). However, experiments do not tell anything about which of the two species will win in a homogeneous system. Two chemostat cultures of *Microcystis* (cf. legend to Fig. 2) were able to approach steady-state growth ($\mu = 0.4 \cdot d^{-1}$) before *Staurastrum* ($\mu = 0.4 \cdot d^{-1}$) was added (open arrow) to the cultures (Fig. 2). In both cultures, *Staurastrum* biomass increased during the following week, whereas the *Microcystis* biomass decreased. From the 14th day (cf. Fig. 2, solid arrow) and onward, one of the cultures (solid curves) was supplied with one pulse of P daily while being diluted continuously with P-free medium. As shown, *Microcystis* responded positively and immediately to this change in treatment, and *Staurastrum* decreased in biomass after a few days. In the other culture, which was supplied continuously with P (broken curve), *Staurastrum* approached steady-state growth, whereas *Microcystis* decreased steadily.

These results reveal that *Staurastrum* is able to outcompete *Microcystis* in chemostats supplied continuously with phosphate, but not when phosphate supply is pulsed. The ability of a species to compete for P, when it is limiting, cannot be evaluated from its ability to grow at low average ambient concentrations. If the alga is exposed to temporary P gradients, its ability to take up P rapidly is of fundamental importance in competition (Grenney et al. 1973; Turpin and Harrison 1979; Turpin et al. 1981; Scavia et al. 1984; Sommer 1984).

Discussion

Our studies have demonstrated that nutrient status can yield important ecological information on phytoplankton blooms. These studies also show that results must be evaluated carefully. The species dependence of the N/C ratio and the P/C ratio, in particular, presents obvious pitfalls in interpretation. Variations in these ratios may at times be caused by shifts in species composition rather than nutrient status. In general,

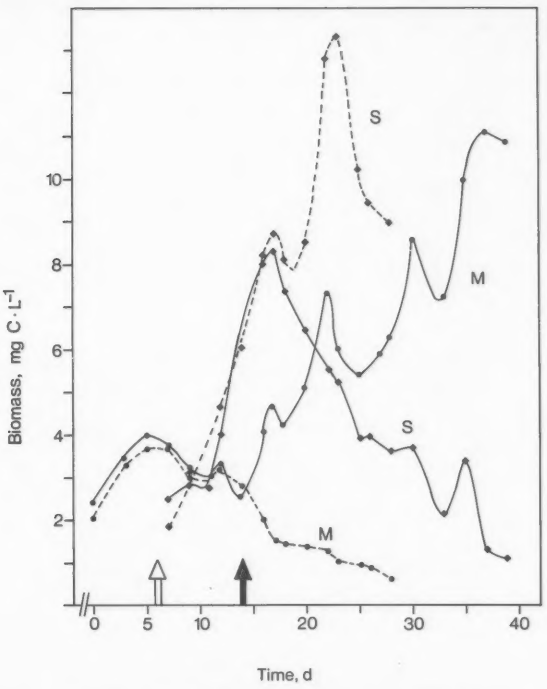


FIG. 2. Competition for phosphate in mixed continuous cultures of *Staurastrum* (◆S) and *Microcystis* (●M). *Staurastrum* was added at day 6 (open arrow) to both cultures. At day 14 (solid arrow), one culture (solid curves) was pulsed once a day with phosphate while being diluted continuously with P-free medium, whereas the other (broken curve) was diluted continuously with 2 μmol $PO_4 \cdot L^{-1}$ medium throughout the experimental period. Culture conditions were otherwise as described for Fig. 1.

conclusions based on nutrient status measurements are best when blooms are nearly monospecific. Nutrient deficiency appears to be most pronounced at peak biomass levels. This result is expected if we assume a relatively constant supply of "new" nutrients. At peak biomass levels, other nutrients may be at subsaturation levels. This is likely to happen if the nutrient supply ratio is not too far from the ratio preferred by the algae. This is, of course, not contrary to the concept of a threshold model for nutrient limitation. Grazing and sinking regulate the biomass quite independently of nutrient supply.

In general, freshwaters appear to be strongly P limited. Brackish waters may exhibit the same property, but P limitation is dampened with increasing salinity. Full-salinity seawater may be clearly N limited or fairly balanced with N and P relative to the average requirement of multispecies phytoplankton communities. It is noteworthy that the addition of sewage, through its low N/P ratio, causes marine systems to become more N limited and fresh and brackish water systems less clearly P limiting. Extreme cases, in which freshwater becomes N limiting (Smith 1983), can be interpreted primarily as a sign of extensive pollution by organic waste. Clear N limitation may, thus, simply be a secondary effect of pollution in many cases.

The variation in species-dependent balance point for N and P indicates that different species have different strategies for nutrient competiton. Nutrient status measurements on multi-specific communities cannot at present yield information at the species level. This problem pertains to a large part of the world's waters, e.g. vast stretches of open ocean that are characterized by oligotrophy and high species diversity. Meanwhile, important knowledge can be gained at the species level from laboratory experiments, as the uptake and competition experiments presented here illustrate. The capacity to take up nutrients is a function of starvation. Just as important, this capacity is species dependent. This implies that the outcome of competition can be directed or determined by the mode of nutrient supply. Nutrient-limited species with a high uptake capacity will have an advantage when the nutrient supply is pulsed.

Acknowledgements

Publication costs were provided by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI 48104. We thank Kjersti Andresen and Marte Morkved for technical assistance.

References

DROOP, M. R. 1974. The nutrient status of algal cells in continuous culture. J. Mar. Biol. Assoc. U.K. 54: 825–855.

GARGAS, E. 1975. Nitrogen and phosphorus as growth limiting factors in a shallow fjord system. Vatten 1975: 56–63.

GOLDMAN, J. C., AND P. M. GLIBERT. 1982. Comparative rapid ammonium uptake by four species of marine phytoplankton. Limnol. Oceanogr. 27: 814–827.

GOLDMAN, J. C., J. J. MCCARTHY, AND D. G. PEAVEY. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature (Lond.) 279: 210–215.

GOTHAM, I. J., AND G-Y. RHEE. 1981a. Comparative kinetic studies of nitrate-limited growth and nitrate uptake in phytoplankton in continuous culture. J. Phycol. 17: 309–314.

1981b. Comparative kinetic studies of phosphate-limited growth and phosphate uptake in phytoplankton in continuous culture. J. Phycol. 17: 257–265.

GRANÉLI, E. 1981. Bioassay experiments in the Falsterbo Channel — nutrients added daily. Kiel. Meeresforsch. Sonderheft. 5: 82–90.

GRENNEY, W. J., D. A. BELLA, AND H. C. CURL, JR. 1973. A theoretical approach to interspecific competition in phytoplankton communities. Am. Nat. 107: 405–425.

HAUG, A., S. MYKLESTAD, AND E. SAKSHAUG. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. I. The chemical composition of phytoplankton populations. J. Exp. Mar. Biol. Ecol. 11: 15–26.

HEALEY, F. P., AND L. L. HENDZEL. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442–453.

HEGSETH, E. N., AND E. SAKSHAUG. 1983. Seasonal variation in light- and temperature-dependent growth of marine planktonic diatoms in in situ dialysis cultures in the Trondheimsfjord, Norway (63°N). J. Exp. Mar. Biol. Ecol. 67: 199–220.

JACKSON, G. A. 1980. Phytoplankton growth and zooplankton grazing in oligotrophic oceans. Nature (Lond.) 284: 439–441.

JENSEN, A., AND E. SAKSHAUG. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. II. Chloroplast pigments in relation to abundance and physiological state of the phytoplankton. J. Exp. Mar. Biol. Ecol. 11: 137–155.

KILHAM, P., AND S. S. KILHAM. 1980. The evolutionary ecology of phytoplankton, p. 571–597. *In* I. Morris [ed.] Physiological ecology of phytoplankton. Blackwell Scientific Publications, London and New York.

LEHMAN, J. T., AND D. SCAVIA. 1982. Microscale patchiness of nutrients in plankton communities. Science (Wash., DC) 216: 729–730.

MCCARTHY, J. J., AND J. C. GOLDMAN. 1979. Nitrogenous nutrition of marine phytoplankton in nutrient depleted waters. Science (Wash., DC) 203: 670–672.

MYKLESTAD, S. 1977. Production of carbohydrates by marine planktonic diatoms. II. Influence of the N/P ratio in the growth medium on the assimilation ratio, growth rate, and production of cellular and extracellular carbohydrates by *Chaetoceros affinis* var. *willei* (Gran) Hustedt and *Skeletonema costatum* (Grev.) Cleve. J. Exp. Mar. Biol. Ecol. 29: 161–179.

MYKLESTAD, S., AND E. SAKSHAUG. 1983. Alkaline phosphatase activity of

Skeletonema costatum populations in the Trondheimsfjord. J. Plankton Res. 5: 557–564.

NALEWAJKO, C., AND D. R. S. LEAN. 1980. Phosphorus, p. 235–258. *In* I. Morris [ed.] Physiological ecology of phytoplankton. Blackwell Scientific Publications, London and New York.

NIEMI, A. 1979. Bluegreen algal blooms and N:P ratio in the Baltic Sea. Acta Bot. Fenn. 110: 59–61.

OLSEN, Y., A. JENSEN, AND H. REINERTSEN. 1985. ATP changes in P-starved algae as a measure of P-deficiency and the growth rate. Int. Ver. Theor. Angew. Limnol. 22: 2866–2871.

OLSEN, Y., A. JENSEN, H. REINERTSEN, AND B. RUGSTAD. 1981. Studies of algal communities in plastic enclosures. Consequences of addition of zooplankton or fish. Report, Norw. Res. Council for Science and Technology, EU 4/81. ISBN 82-7224-177-3. (In Norwegian)

1983a. Comparison of different algal carbon estimates by use of the Droop-model for nutrient limited growth. J. Plankton Res. 5: 43–51.

OLSEN, Y., G. KNUTSEN, AND T. LIEN. 1983b. Characteristics of phosphorus limitation in *Chlamydomonas reinhardtii* (Chlorophyceae) and its palmelloids. J. Phycol. 19: 313–319.

PAASCHE, E. 1973. Silicon and the ecology of marine diatoms. I. *Thalassiosira pseudonana* (*Cyclotella nana*) grown in chemostat with silicate as limiting nutrient. Mar. Biol. 19: 117–126.

PASCIAK, W. J., AND J. GAVIS. 1974. Transport limitation of nutrient uptake in phytoplankton. Limnol. Oceanogr. 19: 881–888.

REDFIELD, J. L., B. H. KETCHUM, AND F. A. RICKARDS. 1963. The influence of organisms on the composition of seawater, p. 26–77. *In* M. N. Hill [ed.] The sea. 2. John Wiley & Sons, New York, NY.

RHEE, G-Y. 1973. A continuous culture study of phosphate uptake, growth rate and polyphosphate in *Scenedesmus* sp. J. Phycol. 9: 495–506.

1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnol. Oceanogr. 23: 10–25.

RYTHER, J. H., AND W. M. DUNSTAN. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science (Wash., DC) 171: 1008–1013.

SAKSHAUG, E. 1977a. Limiting nutrients and maximum growth rates for diatoms in Narragansett Bay. J. Exp. Mar. Biol. Ecol. 28: 109–123.

1977b. Plantenæringsstoffer og klorofyll *a*, p. 135–151. *In* E. Lande [ed.] Resipientundersøkelsen i Trondheimsfjorden 1972–1975. University of Trondheim, The Museum, Zool. Series 1977: 11. (In Norwegian)

1978. The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton. D.Sc. thesis, University of Trondheim, Trondheim, Norway. 83 p.

SAKSHAUG, E., K. ANDRESEN, S. MYKLESTAD, AND Y. OLSEN. 1983. Nutrient status of phytoplankton communities in Norwegian waters (marine, brackish, and fresh) as revealed by their chemical composition. J. Plankton Res. 5: 175–196.

SAKSHAUG, E., E. GRANÉLI, M. ELBRACHTER, AND H. KAYSER. 1984. Chemical composition and alkaline phosphatase activity of nutrient-saturated and P-deficient cells of four marine dinoflagellates. J. Exp. Mar. Biol. Ecol. 77: 241–254.

SAKSHAUG, E., AND O. HOLM-HANSEN. 1977. Chemical composition of *Skeletonema costatum* (Grev.) Cleve and *Pavlova* (*Monochrysis*) *lutheri* (Droop) Green as a function of nitrate-, phosphate-, and iron-limited growth. J. Exp. Mar. Biol. Ecol. 29: 1–34.

1984. Factors governing pelagic production in polar oceans, p. 1–18. *In* O. Holm-Hansen, L. Bolis, and R. Gilles [ed.] Marine phytoplankton and productivity. Lecture notes on coastal and estuarine studies, Vol. 8. Springer Verlag, Berlin, London, and New York.

SAKSHAUG, E., AND S. MYKLESTAD. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. III. Dynamics of phytoplankton blooms in relation to environmental factors, bioassay experiments and parameters for the physiological state of the populations. J. Exp. Mar. Biol. Ecol. 11: 157–188.

SAKSHAUG, E., S. MYKLESTAD, K. ANDRESEN, E. N. HEGSETH, AND L. JØRGENSEN. 1981. Phytoplankton off the Møre coast in 1975–1976: distribution, species composition, chemical composition, and conditions for growth, p. 682–711. *In* R. Sætre and M. Mork [ed.] The Norwegian coastal current. University of Bergen, Bergen, Norway.

SCAVIA, D., G. L. FAHNENSTIEL, J. A. DAVIS, AND R. G. KREIS, JR. 1984. Small-scale nutrient patchiness: some consequences and a new encounter mechanism. Limnol. Oceanogr. 29: 785–793.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Sciences (N.Y.) 95: 260–262.

SMAYDA, T. J. 1974. Bioassay of the growth potential of the surface water of lower Narragansett Bay over an annual cycle using the diatom *Thalassiosira pseudonana* (oceanic clone, 13-1). Limnol. Oceanogr. 19: 889–901.

SMITH, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science (Wash., DC) 221: 669–671.

SOLÓRZANO, L., AND J. D. H. STRICKLAND. 1968. Polyphosphate in seawater. Limnol. Oceanogr. 13: 515–518.

SOMMER, U. 1984. The paradox of the plankton: fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-trough cultures. Limnol. Oceanogr. 29: 633–636.

TILMAN, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58: 338–348.

TILMAN, D., S. S. KILHAM, AND P. KILMAN. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 348–372.

TURPIN, D. H., AND P. J. HARRISON. 1979. Limiting nutrient patchiness and its role in phytoplankton ecology. J. Exp. Mar. Biol. Ecol. 39: 151–166.

TURPIN, D. H., J. S. PARSLOW, AND P. J. HARRISON. 1981. On limiting nutrient patchiness and phytoplankton growth: a conceptual approach. J. Plankton Res. 3: 421–431.

Nutrient Enrichment Studies in a Coastal Plain Estuary: Phytoplankton Growth in Large-Scale, Continuous Cultures[1]

Christopher F. D'Elia

Chesapeake Biological Laboratory, Center for Environmental and Estuarine Studies, University of Maryland, P.O. Box 38, Solomons, MD 20688-0038, USA

James G. Sanders

Benedict Estuarine Research Laboratory, Academy of Natural Sciences, Benedict, MD 20612, USA

and Walter R. Boynton

Chesapeake Biological Laboratory, Center for Environmental and Estuarine Studies, University of Maryland, P.O. Box 38, Solomons, MD 20688-0038, USA

D'Elia, C. F., J. G. Sanders, and W. R. Boynton. 1986. Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures. Can. J. Fish. Aquat. Sci. 43: 397–406.

The response of phytoplanktonic growth to experimental nutrient addition in a tributary of the Chesapeake Bay estuary varied with season and nutrient availability. In bioassay experiments employing outdoor 0.5-m^3 continuous cultures freshly inoculated with natural phytoplankton from the Patuxent River estuary, supplements of N, either as ammonium or nitrate, enhanced growth greatly during the low-flow, late-summer season — a period when N:P ratios of dissolved inorganic nutrient standing stocks are characteristically below 5:1 (by atoms). Growth response to N addition was very rapid (1 d after the start of an experiment), implying that phytoplankton in the bioassay were N limited when removed from the estuary. PO_4^{3-} addition enhanced phytoplankton growth during the late-winter, high-flow season, when N:P ratios (as previous) typically exceed 90:1 (by atoms), but the response lagged enrichment by at least 4 d and biomass levels achieved in these cultures were less than one third of those achieved in the N-enriched cultures during the late summer. The great seasonal variability in river flow, nutrient regimes, and the response of natural phytoplankton assemblages to nutrient enrichment in the Patuxent, and similar estuaries, suggest that management strategies to improve "water quality" will need to consider N as well as P additions.

La croissance du phytoplancton suite à l'addition expérimentale de substances nutritives dans un tributaire de l'estuaire de la baie Chesapeake a varié selon la saison et la disponibilité desdites substances. Lors de tests biologiques faits en utilisant des cultures extérieures en continu de 0,5 m^3 fraîchement inoculées par du phytoplancton naturel venant de l'estuaire de la rivière Patuxent, des suppléments d'azote, sous forme d'ammonium ou de nitrate, on entraîné une forte croissance pendant la période d'étiage à la fin de l'été, période où les rapports N:P des substances nutritives inorganiques dissoutes sont de façon caractéristique inférieurs à 5:1 (par atome). La croissance s'est faite très rapidement après l'addition d'azote (1 journée après le début de l'expérience), ce qui signifie que le phytoplancton utilisé dans le test biologique était limité par l'azote au moment de son prélèvement dans l'estuaire. L'addition de PO_4^{3-} a augmenté la croissance de phytoplancton pendant la période de crues à la fin de l'hiver, au moment où les rapports N:P (comme ceux qui précèdent) dépassent de façon typique 90:1 (par atome), mais la réponse s'est fait attendre au moins 4 jours et les biomasses obtenues dans ces cultures équivalaient à moins de un tiers de celles obtenues dans les cultures enrichies à l'azote à la fin de l'été. La grande variabilité saisonnière du débit de la rivière, le régime des substances nutritives et la réponse des groupes d'organismes phytoplanctoniques naturels à l'accroissement des substances nutritives dans la rivière Patuxent et dans des estuaires similaires donnent à penser que les stratégies de gestion visant à améliorer la « qualité de l'eau » devront tenir compte aussi bien des ajouts d'azote que de phosphore.

Received November 26, 1984
Accepted August 8, 1985
(J8028)

Reçu le 26 novembre 1984
Accepté le 8 août 1985

The effect of anthropogenic nutrient enrichment on primary productivity is a topical concern in many estuaries and coastal systems (Gray and Paasche 1984; Price et al. 1985). Chesapeake Bay, the largest estuary in the United States, now shows enough symptoms of overenrichment (Heinle et al. 1980; Brush 1984; Officer et al. 1983; Price et al. 1985) to warrant concern about regulating nutrient inputs. However, the dogma that primary productivity is typically P limited in freshwaters (Schelske and Stoermer 1972; Schindler 1977, 1981) and N limited in marine waters (Ryther and Dunstan 1971; Thomas et al. 1974; Bishop et al. 1984) is difficult to reconcile for estuaries. Accordingly, great uncertainty exists over whether to reduce P or N inputs.

Several approaches have been used to assess nutrient limitation of phytoplankton growth in natural waters. The approaches fall into four categories: (1) "physiological," in which some

[1]This paper was presented at the Phosphorus–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharine's, Ont., May 1984.

metabolic characteristic is assayed to indicate nutrient limitation; (2) "mathematical," in which statistical (Vollenweider 1976) or dynamic, numerical models (O'Connor et al. 1977; O'Connor 1981) are used to evaluate presumed response to nutrient loading; (3) "stoichiometric," in which the relative availability of inorganic nutrients in loadings (Jaworski et al. 1972; Jaworski 1981) or in dissolved or particulate standing stocks in the water are taken to indicate nutrient limitation or repletion; and (4) "growth bioassay," in which changes in plant biomass are evaluated when nutrients are added to phytoplankton cultures (Ryther and Dunstan 1971; Maestrini et al. 1984a), enclosed natural phytoplankton assemblages (reviewed by Schelske 1984), or entire ecosystems (Schindler and Fee 1974).

Most regulatory and resource management agencies concerned with developing nutrient control strategies rely heavily on dynamic water-quality models. However, as Maestrini et al. (1984a, 1984b) and Schelske (1984) have emphasized, the growth–bioassay approach provides the best evidence for determining nutrient limitation of primary productivity in natural waters. Previous enrichment studies have used test algal bioassays in well-mixed estuaries (Type "A," by the classification of Pritchard 1955) characterized by relatively low inputs of freshwater. For example, in Narragansett Bay, Rhode Island, Smayda (1974) found evidence of N but not P limitation, as might be expected for coastal waters (Ryther and Dunstan 1971).

Type "B" estuaries such as Chesapeake Bay exhibit much stronger seasonal variations in freshwater flow and nutrient regimes, implying seasonal variations in nutrient limitation (Boynton et al. 1982). The Bay and its major tributaries are characterized by large winter–spring inputs of freshwater containing a surplus of N relative to P compared with that of typical phytoplanktonic needs (Redfield 1934). During the late-summer, low-flow season, sediment and water column recycling play a proportionately larger role in supplying nutrients (Kemp and Boynton 1984). Nutrients derived from sediments are quantitatively most important during that season and have surplus of P to N relative to typical phytoplanktonic needs (Kemp and Boynton 1984).

Our experimental study examines the relationship between nutrient inputs and phytoplankton productivity in the mesohaline region of a Chesapeake Bay tributary, the Patuxent River, Maryland. Our primary objective was to assess annual variations in N or P limitations. Our approach was a variant of the enrichment bioassay approach (category 4, see above) in which we inoculated large-scale, continuous phytoplankton cultures with indigenous phytoplankton assemblages and monitored their response to nutrient additions.

Methods

Experiments were repeated (10 times) between June 1983 and October 1984. Frequent repetition of comparable experiments seemed necessary to address the considerable interseasonal and interannual variability characteristic of the estuary.

Study Site

The experiments were conducted at the Benedict Estuarine Research Laboratory, Benedict, Maryland (river km 30). The Patuxent Basin, which is located between Washington, D.C., and Baltimore, Maryland, has undergone extensive urbanization with a daily sewage input of about 1.33×10^3 $m^3 \cdot d^{-1}$ and a base flow of approximately 30 $m^3 \cdot d^{-1}$ (Jaworski 1981). Point-source nutrient loading to the river on a flow-weighted basis approximates that for the Potomac River to the south. Nearly a doubling of sewage inputs is projected in the next two decades and the area of the river near the study site has been identified as critical for purposes of evaluating the nutrient control strategy developed in the Sec. 208 Basin Plan (Office of Environmental Programs 1982). The annual salinity range in the study area is from 6 to 16‰, with a median of approximately 10‰.

Experimental Rationale

We chose a continuous culture approach similar to that of Goldman and Ryther (1975), D'Elia et al. (1977), and Sanders et al. (1981) instead of a batch approach for several reasons. First, cell densities in the cultures are maintained at levels closer to natural levels. Thus, light limitation or the production of allelopathic substances is less likely. Second, nutrients are supplied continuously rather than as an initial dosing to maintain concentrations in a more restricted and realistic range. Third, continuous cultures can be sustained longer — a feature useful in understanding species succession effects. Finally, continuous cultures prove particularly amenable to studies of effects on community structures (Tilman et al. 1982). Additional details regarding continuous mass outdoor algal culture can be found elsewhere (e.g. Goldman 1979a, 1979b; Maestrini et al. 1984a, 1984b).

Before an experiment, all culture tanks were acid washed (10% HCl) and then rinsed twice with fresh water; all air, water, and nutrient delivery hosing was replaced. Natural phytoplankton assemblages were inoculated into fiberglass tanks (0.5-m^3 volume; 0.37-m diameter) held under natural light and temperature conditions. Treatments were in triplicate. The 12 tanks were filled sequentially in 2- to 3-min "bursts" to ensure that homogeneous sampling occurred. The raw river water used contained natural phytoplankton assemblages, but was screened through 35-μm mesh to remove most zooplankton. This also removed larger phytoplankton, a small portion of the plant biomass. Dilution flows were started immediately after filling, air was bubbled gently to mix the tanks, and each tank was sampled for in vivo chlorophyll *a* fluorescence, species composition, cell counts, and influent and residual nutrient concentrations.

The culture tanks were continuously diluted using river water filtered to 1 μm. The dilution water and nutrient enrichment medium were pumped at precise rates using peristaltic pumps. We chose a dilution rate of 0.5 culture volumes $\cdot d^{-1}$ to maintain cell densities in control tanks similar to river populations. Measured dilution rates varied within ±2% of the nominal rate.

A "standard" experiment, i.e. one designed to test the N- or P-limited algal growth potential at $0.5 \cdot d^{-1}$ dilution rate, was as follows: three "control" cultures (diluted by only filtered river water); three P-enriched cultures (diluted by filtered river water and nutrient stock to achieve a composite input level of 10 μmol PO_4^{3-}-$P \cdot L^{-1}$ and ambient dissolved N); three ammonium-enriched cultures (diluted by filtered river water and nutrient stock to achieve a composite input level of 50 μmol $NH_4^+ \cdot L^{-1}$ and ambient dissolved P); and three nitrate-enriched cultures (diluted by filtered river water and nutrient stock to achieve a composite input enrichment of

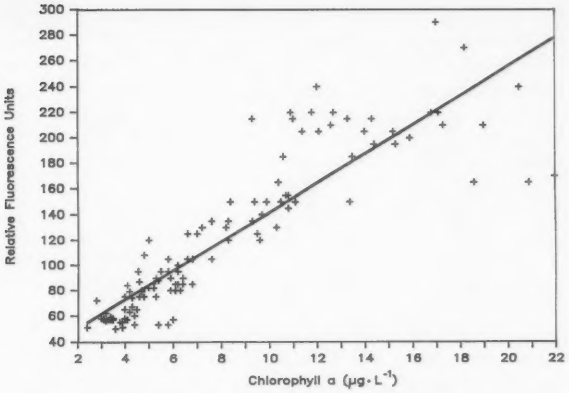


FIG. 1. Scatter plot of chlorophyll *a* vs. in vivo relative chlorophyll fluorescence during an experiment in March 1984. Data represent all tanks, regardless of experimental treatment.

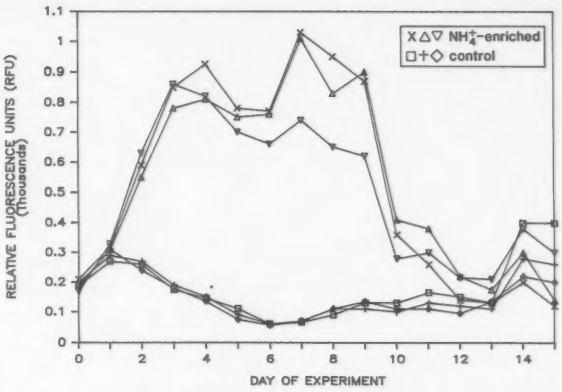


FIG. 2. Experimental replicability: biomass (expressed as in vivo relative chlorophyll fluorescence, RFU) changes during replicate NH_4^+-enriched and control (unenriched) treatments in an experiment in August 1984.

50 μmol $NO_3^- \cdot L^{-1}$ and ambient dissolved P). Actual "residual" dissolved nutrient concentrations achieved in the tanks depended, of course, on (1) the amount of nutrient that was taken up and assimilated into phytoplankton biomass, (2) the influent nutrient concentration, and (3) the dilution rate of the culture. Nutrient enrichment levels were chosen to ensure that excess, but not environmentally unrealistic, nutrient levels were maintained in the cultures.

Sampling

The individual tanks and the river were sampled at 13:00. Phytoplankton samples were preserved with Utermöhl's solution (buffered iodine), settled, and enumerated by inverted microscopy (Utermöhl 1958). Most of this information will be presented in a sequel to this paper (Sanders et al., in prep.). Each tank was sampled daily for in vivo chlorophyll *a* fluorescence. Approximately 25 mL was taken from the center of each tank and fluorescence determinations made using a Turner Designs model 10 fluorometer equipped with Corning CS-560 excitation and Wratten No. 25 emission filters.

To calibrate in vivo chlorophyll *a* fluorescence, samples were filtered biweekly on Whatman GF/F glass-fiber filters (nominal porosity ~0.7 μm) for subsequent extraction of chlorophyll *a*. The filters were frozen until they were extracted using dimethylsulfoxide (DMSO) − acetone (3:1, vol/vol). Correlation coefficients between extracted chlorophyll *a* and relative fluorescence (all experimental treatments included) were strongly positive within ($r = 0.89$ for the experiment of March 1984; Fig. 1) and among experiments ($r = 0.88$ for three experiments from February to May 1984; not shown). Accordingly, we conclude as have others (Goldman et al. 1973; Thomas et al. 1974; D'Elia et al. 1977) that relative fluorescence provides a reasonable and efficient method of estimating biomass and growth in enrichment experiments.

We report biomass in terms of relative in vivo fluorescence (RFU) because (1) RFU and chlorophyll *a* correlate well (Fig. 1) and (2) we sampled more frequently for RFU. One may apply a rough conversion of approximately 13 RFU · μg chlorophyll $a \cdot L^{-1}$.

We did not do routine comparisons of filtered and whole-water fluorescence, but the close correlation between chlorophyll *a* and RFU and the low value of the ordinal intercept in scatter plots of the two characteristics (Fig. 1) seem to preclude high levels of "dissolved" fluorescence.

For dissolved nutrient and chlorophyll *a* measurements, water was filtered through acid-washed Gelman A/E glass-fiber filters and frozen for dissolved nitrate, nitrite, ammonium, phosphate, and silicic acid determinations using standard automated colorimetric procedures (U.S. Environmental Protection Agency 1979).

Replicability

Good within-treatment replicability provides crucial substantiation that the results for any given treatment are not spurious. Replicability in terms of biomass (Fig. 2) and species composition (not shown) is typically remarkably close; experience has shown us that both the homogeneity of the initial tank fill and the precision in the rate of nutrient and dilution water additions account for this. In these experiments, the standard deviation of the mean of initial cell densities varied less than ±15% (not shown); even subsequent to experimental dosing, cell densities in triplicate tanks generally ranged within ±20% of each other in the first week and diverged gradually thereafter, as species composition began to change and fouling organisms appeared.

Since within-treatment variability was generally low and to avoid producing overly complex figure presentations, we present our results below as the mean response obtained in triplicate tanks.

Results

Annual Cycle of Nutrient Availability

To understand the season-to-season variations in response to experimental enrichments, one must consider the accompanying variations in both nutrient concentrations and N:P ratios in the river water from which the phytoplankton were obtained and that was continuously supplied to the tanks at 0.5 culture volumes $\cdot d^{-1}$. The dissolved nutrient standing stocks in influent river water over the study period (June 1983 − October 1984) displayed season-to-season variations typical for mesohaline regions of many estuaries. Concen-

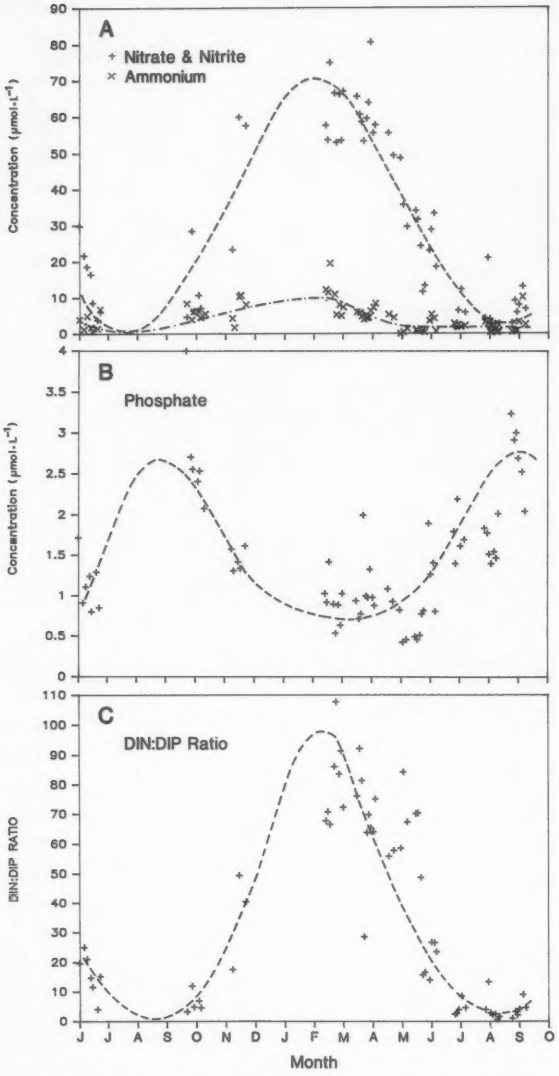


FIG. 3. Nutrient concentrations and ratios in unenriched dilution water to the cultures vs. month, 1983–84. (A) Nitrate + nitrite (summed) and ammonium; (B) phosphate; (C) dissolved inorganic nitrogen (DIN) : dissolved inorganic phosphorus (DIP) ratios. All curves were fitted by eye.

trations of NH_4^+ (Fig. 3A) ranged from less than 1.0 to approximately 18 $\mu mol \cdot L^{-1}$ and were generally somewhat higher during the winter–spring period (5–12 $\mu mol \cdot L^{-1}$) than during warmer portions of the year (<6 $\mu mol \cdot L^{-1}$). $NO_3^- + NO_2^-$ concentrations (Fig. 3A) ranged from less than 1.0 to approximately 70 $\mu mol \cdot L^{-1}$, with highest concentrations associated with periods of highest river discharge (winter–spring). Concentrations of dissolved inorganic phosphorus (DIP) exhibited a distinct summer maximum (2–4 $\mu mol \cdot L^{-1}$), with lower concentrations (0.5–1.0 $\mu mol \cdot L^{-1}$) evident for the remainder of the year (Fig. 3B), similar to the patterns reported by Taft and Taylor (1976) and Pilson et al. (1980).

DIP levels generally exceed levels typically thought to be growth limiting for phytoplankton, while dissolved inorganic nitrogen (DIN) levels decline to growth-limiting concentrations only during the late summer (August–September). The relative constancy on a day-to-day basis of nutrient concentrations suggests that the resupply of dissolved inorganic nutrients to the water column is in approximate balance, over the short term, with utilization and removal.

DIN:DIP ratios in water column standing stocks vary enormously over the annual period (Fig. 3C). Highest values (~100:1) are obtained during the high-flow, late-winter period and suggest in comparison with the "Redfield ratios" of 16:1 (Redfield 1934) that relative to P, N availability during this period exceeds phytoplanktonic requirements. Lowest values (~1:1) are obtained during the low-flow, late-summer period, suggesting that stoichiometrically, P availability exceeds requirements then.

Biomass Responses to Experimental Conditions

The responses to enrichment fell into one of three categories: (1) immediate and strong, (2) delayed and weak, or (3) slight or negligible. Such responses seem to be characteristic of different seasons and river flow regimes, and the immediacy of response seems pertinent to the nutritional status of the phytoplankton assemblages isolated from the river.

Initial conditions in the tanks and results of the enrichment experiments are summarized in Table 1. During the late summer and fall, nutrient enrichment produced immediate and pronounced responses to N (both NH_4^+ and NO_3^-). Late fall and winter experiments generally produced delayed and weak responses to P. Late spring and early summer enrichments produced slight or negligible effects. River and control biomass levels were lowest especially during high-flow, colder seasons, and experimental treatment biomass were highest during the warmer, lower flow seasons. Examples are given below.

When DIN concentrations were low and DIP concentrations were high (August–September), there was a strong and rapid response to DIN enrichment. With either NH_4^+ or NO_3^-, biomass levels rose to approximately twice that of controls withn a day of enrichment with NO_3^- or NH_4^+ (Fig. 4A). P-enriched tanks did not show response with biomass attained following that in control tanks (Fig. 4A).

An effective way to assess relative responses is to plot the daily ratio of mean biomass (RFU) in comparably enriched tanks against that in unenriched control tanks. Both time series (day-to-day) (Fig. 4B) and treatment versus treatment ("ratio:ratio") (Fig. 4C) comparisons are easily made. This highlights differences between experimental and control treatments, and yields a ratio of 1.0 in the absence of a nutrient effect and a higher ratio if the nutrient stimulates growth, as was the case for NO_3^- and NH_4^+ data (Fig. 4B, 4C).

Midwinter experiments exhibited a weak and delayed response to P. For example, during the experiment of February 1984, biomass response occurred late in the experiment, days 8–18 (Fig. 5A). Biomass gradually increased to approximately three times that in control tanks and remained high through the experiment's end (Fig. 5B). Assemblages receiving either NO_3^- or NH_4^+ enrichment were comparable with controls. The ratio:ratio plot (Fig. 5C) clearly shows the response to P, but not to N.

Late spring through early summer is characterized by high DIN and DIP concentrations in the river and DIN:DIP ratios

TABLE 1. Initial residual nutrient concentrations ($\mu mol \cdot L^{-1}$), dominant species, and general algal growth responses in the tanks during experiments conducted in 1984. DIN = dissolved inorganic nitrogen (nitrate + nitrite + ammonium); DIP = dissolved inorganic phosphorus.

Date	Enrichment	Residual nutrients [DIN]	Residual nutrients [DIP]	First dominant (% of cells)	Second dominant (% of cells)	Third dominant (% of cells)	Growth response
Feb. 10	None	69.4	0.64	*Chaetoceros* sp. (32.6)	*Skeletonema costatum* (14.6)	<30-μm centrics (8.6)	Weak P
	Ammonium	93.7	0.63	(27.0)	(15.2)	(6.5)	
	Nitrate	85.9	0.67	(25.9)	(13.0)	(11.8)	
	Phosphate	60.4	9.33	(27.6)	(13.9)	(12.6)	
Mar. 14	None	97.2	0.57	<30-μm centrics (22.0)	*Katodinium rotundatum* (25.0)	*Cryptomonas* sp. (11.7)	None
	Ammonium	108.0	0.61	(16.5)	(25.9)	(13.8)	
	Nitrate	108.0	0.59	(19.1)	(17.9)	(13.6)	
	Phosphate	83.9	6.13	(16.3)	(24.3)	(14.9)	
May 16	None	64.6	0.37	*Thalassiosira pseudonana* (38.6)	<30-μm centrics (24.9)	*S. costatum* (22.0)	None
	Ammonium	92.2	0.24	(39.1)	(26.5)	(22.8)	
	Nitrate	101.0	0.33	(35.4)	(25.8)	(22.0)	
	Phosphate	55.4	9.20	(40.5)	(22.7)	(21.0)	
July 26	None	8.84	1.75	*Thalassiosira* sp. (21.1)	<30-μm centrics (13.0)		Medium N
	Ammonium	38.4	0.69	(22.0)	(23.7)		
	Nitrate	48.9	1.48	(29.3)	(13.7)		
	Phosphate	3.3	10.9	(28.7)	(14.2)		
Aug. 24	None	3.17	2.93	*S. costatum* (17.1)	*Thalassiosira* sp. (12.8)	Small flagellates (19.5)	Strong N
	Ammonium	45.0	2.49	(12.2)	(16.8)	(22.1)	
	Nitrate	50.1	2.71	(11.6)	(15.1)	(18.9)	
	Phosphate	2.07	14.5	(18.4)	(11.8)	(22.8)	
Sept. 17	None	6.89	2.15	*S. costatum* (40.8)	*Thalassiosira* sp. (21.3)	Cryptomonads (3.9)	Strong N
	Ammonium	45.7	1.67	(39.7)	(23.0)	(3.5)	
	Nitrate	48.3	1.82	(42.0)	(23.0)	(3.4)	
	Phosphate	2.28	12.6	(39.7)	(23.0)	(2.8)	
Oct. 18	None	27.6	1.67	*Thalassiosira* sp. (20.9)	*Chroomonas* sp. (8.6)	Small flagellates (20.2)	Weak P
	Ammonium	63.4	1.67	(23.1)	(14.6)	(10.2)	
	Nitrate	55.0	1.67	(27.1)	(9.7)	(20.3)	
	Phosphate	15.1	12.6	(22.7)	(8.1)	(19.5)	

that are in rough relative proportion to phytoplanktonic requirements (Fig. 3); response to nutrient addition was negligible. Figure 6A shows the relative fluorescence during an experiment conducted during the late spring (March 14 – April 5). Ammonium-enriched tanks exhibited slightly elevated relative fluorescences from days 5 to 12, and a subsequent decline (Fig. 6B), but in no treatment was there a substantial difference from the control. Ratio:ratio plots show that on the average, little response occurred to any enrichment (Fig. 6C).

A weak or negligible response is also represented in the experiment of May 16 – June 1, 1984. During the first 10 d of the experiment, all treatments tracked river levels closely (Fig. 7A, 7B), presumably varying with insolation. Subsequently, the treatments diverged with no evident response to any nutrient (Fig. 7C).

Discussion

Seasonal Variation in Nutrient Limitation

A seasonal shift from P to N enrichment potential from winter to summer and from N to P from summer to winter is clearly evident in Fig. 8., which summarizes the ranges of June 1983 through October 1984. The maximum response ratios (i.e. the ratio of biomass in experimentally versus unenriched "control" tanks) for N-enriched tanks was achieved during the experment of August 1984 (Fig. 8B, 8C) whereas the maximum response ratio for P was achieved in February 1984 (Fig. 8A). As one would expect from the Redfield ratios, seasonal shifts in growth-stimulation potential for N or P coincide with seasonal shifts in the ratios of ambient nutrient standing stocks in the estuary (Fig. 3). Thus, our study, like others (Lin and Schelske 1981; Schelske et al. 1975; Smayda 1974), clearly shows that a single nutrient element alone may not limit annual productivity. However, we are unaware of any enrichment study for any high-flow estuary showing such distinctive seasonal patterns in response.

During the winter, high-flow regime, our experiments suggested that growth-stimulation potential existed for phosphorus additions, but the magnitude of the increases measured during these experiments was small relative to the summer response to N enrichment. The maximum enrichment response ratio for late-summer N enrichment was nearly 14, four times the maximum achieved in response to P. Moreover, during the summer–fall period, biomass typically doubled rapidly

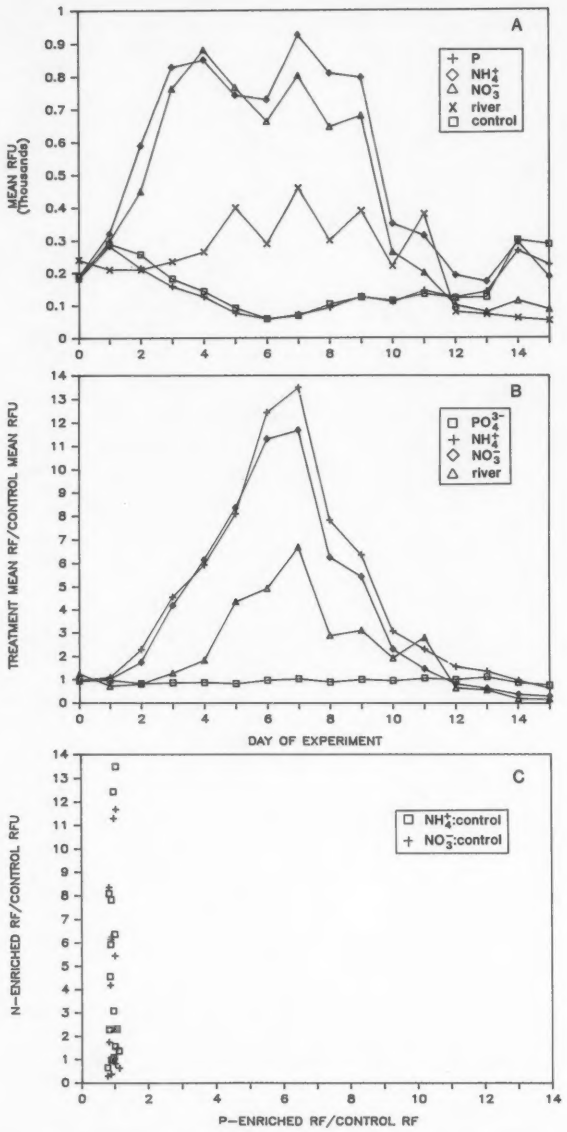


FIG. 4. Immediate and strong response to nitrogen: biomass (expressed as in vivo relative chlorophyll fluorescence, RFU) changes during a "standard" experiment in August 1984. (A) RFU (mean of triplicate tanks and unfiltered Patuxent River water) vs. day after start of experiment; (B) ratio of mean RFU of triplicate experimental tanks to mean of triplicate unenriched control tanks vs. day after start of experiment; (C) ratio of mean RFU of triplicate PO_4^{3-}-enriched experimental tanks to mean of triplicate NO_3^--enriched and NH_4+-enriched tanks on a given day. The greater the range in the x or y direction, the greater the nutrient enrichment potential for the nutrient. River = unfiltered Patuxent River water; control = unenriched tanks.

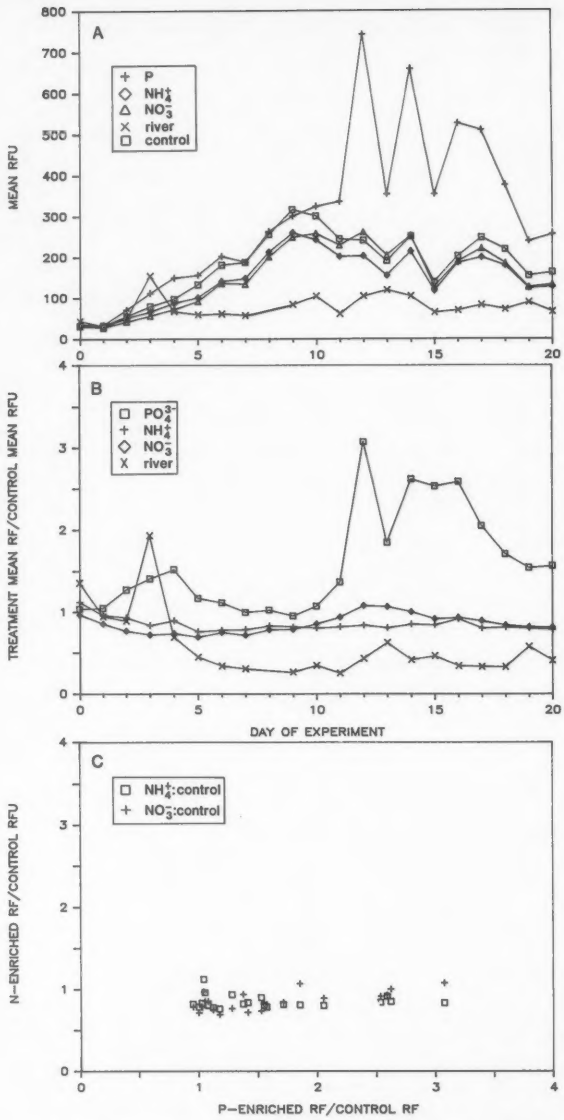


FIG. 5. Delayed and weak response to phosphorus for an experiment in February 1984. Treatments and abbreviations as in Fig. 4.

(within 24–48 h) in N-dosed tanks. Such a rapid response suggests that phytoplankton in the initial inoculum were in a physiological state of N deficiency. Winter responses to P were much slower, sometimes taking 10–15 d to occur. Such slow responses provide little insight regarding the nutritional status of the phytoplankton used in the initial inoculum. Conceivably, this inoculum was nutrient sufficient and the increase during the later stages of the experiment reflected the effect of prolonged confinement in the tanks and the development of P deficiency with time after isolation. Further experimentation would be needed to confirm this speculation.

Interannual Variations in Nutrient Limitation

In estuaries such as the Patuxent, a reasonable hypothesis is that the magnitude and timing of responses varies year to year with the magnitude and timing of such external factors as river flow and total nutrient loading. Grazing (Heinle et al. 1979),

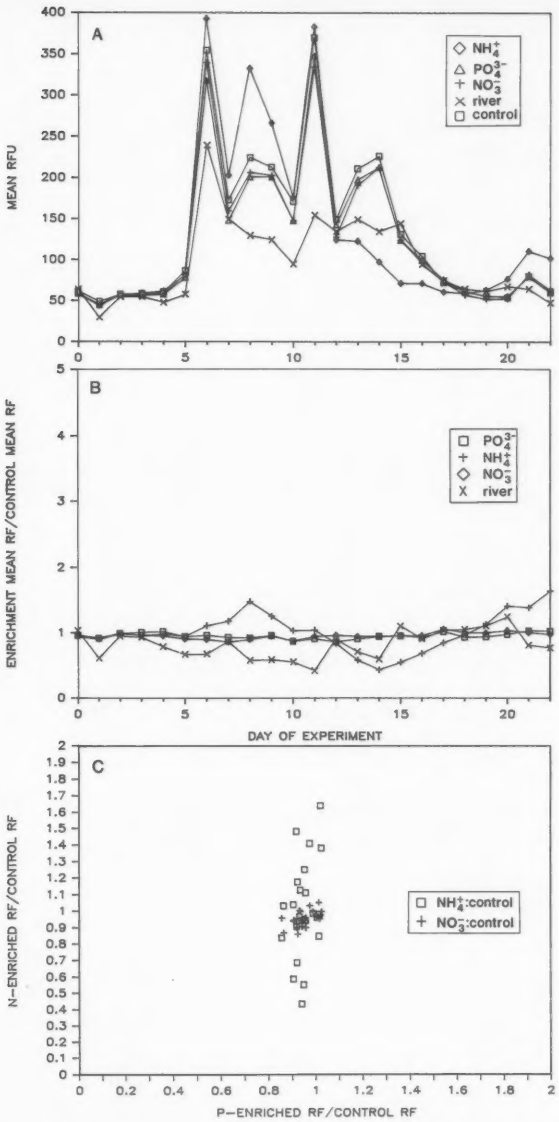


FIG. 6. Weak or negligible response for an experiment in late March 1984. Treatments and abbreviations as in Fig. 4.

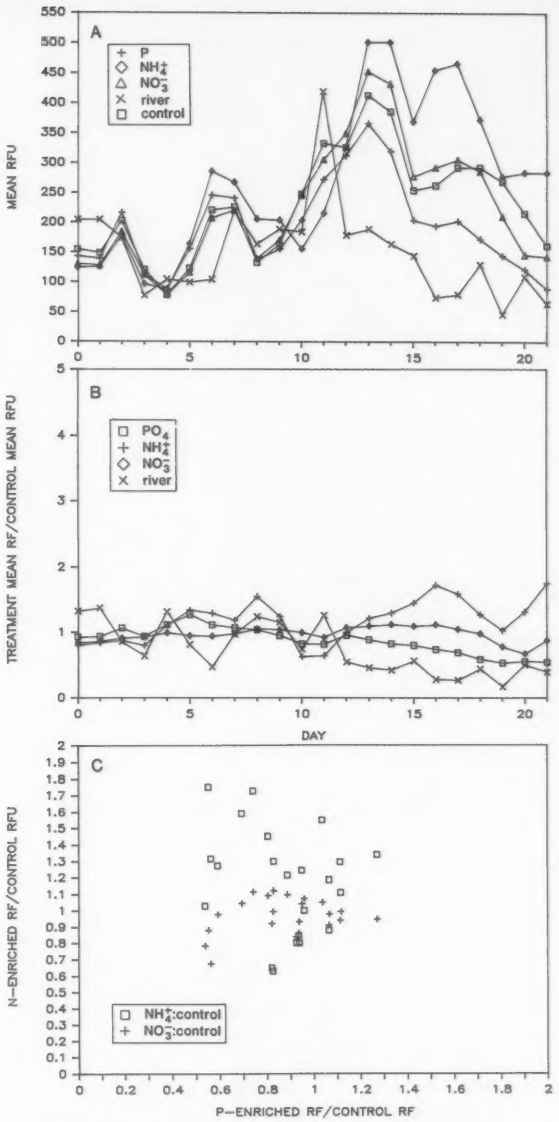


FIG. 7. Weak or negligible response for an experiment in late May 1984. Treatments and abbreviations as in Fig. 4.

the degree of stratification (Webb and D'Elia 1980), turbidity (Keefe et al. 1976), and other factors known to vary interannually in estuaries may further modify the in situ responses of phytoplankton to nutrient enrichment.

One important, yet unresolved, issue is whether responses to N versus P reverse during the highly productive summer period in years of above-normal flow. During high-flow periods, proportionately more N than P enters the estuary due to the greater percentage of N (particulary NO_3^-) transported via nonpoint runoff. In very dry years, external loadings to the river are P rich because of the large amounts of this element relative to N in sewage discharges (Ryther and Dunstan 1971). Some field observations of dissolved N:P ratios also suggest that rapid changes occur with considerable interannual variability in the ratio in the Chesapeake Bay estuary and its tributaries (Boynton et al. 1982). While field and experimental data are not extensive, one might expect considerable interannual variation, particularly in the magnitude of phytoplanktonic responses to nutrient enrichment.

Potential Influences of Light, Grazers, and Nutrient Recycling

This study asks which nutrient element, if any, potentially limits the standing stock of organic matter produced by phytoplankton in the estuarine portion of the Patuxent River. Accordingly, its aim has been to ensure that factors other than nutrient

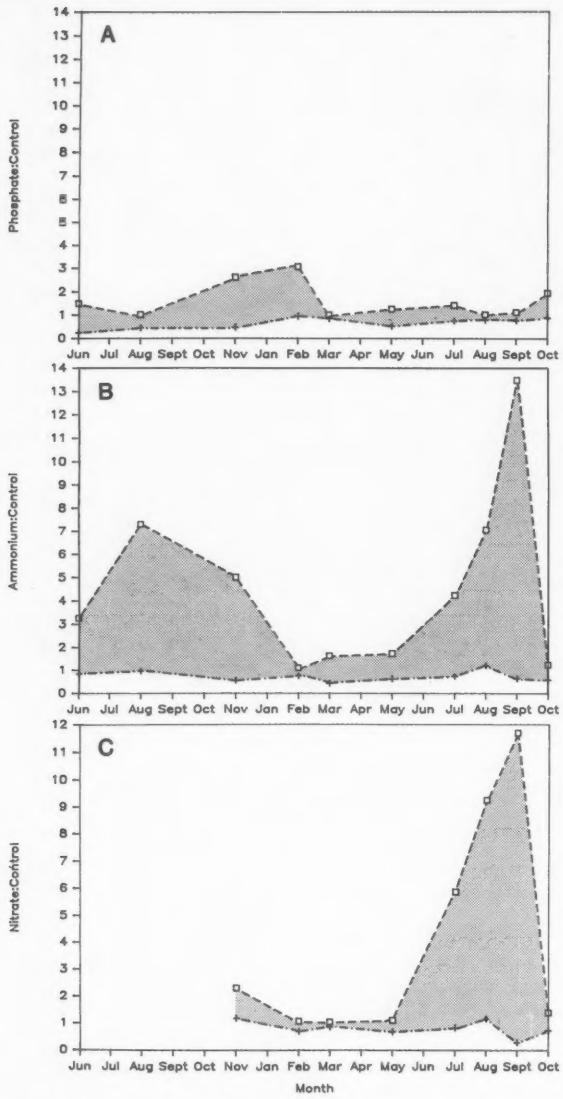


FIG. 8. Range of ratios of RFU of triplicate nutrient-enriched experimental tanks to mean of triplicate unenriched control tanks during each experiment from June 1983 through October 1984. (A) Phosphate-enriched to control; (B) ammonium-enriched to control; (C) nitrate-enriched to control (nitrate enrichments were not done prior to November 1983). The greater the range, the greater the nutrient enrichment potential for the given nutrient.

availability (e.g. grazing) were not limiting phytoplankton standing stocks or complicating our ability to assess and control nutrient inputs to the experimental tanks (e.g. benthic–pelagic interactions). A few comments are warranted about differences between estuarine and experimental conditions to relate our study to "real world" nutrient control strategies.

First, day-to-day fluctuations in biomass in both experimental tanks and the river (e.g. Fig. 4 and 6) suggest that variations in irradiance also have an effect. The correspondence between changes in bimass in the tanks and the river in the spring experiment (Fig. 6) suggested that light limitation was particularly important then. Light levels were generally less attenuated by suspended sediment in the experimental tanks than in the river because all water used to dilute the tanks was fine-filtered to approximately 1 μm. Time-varying model approximations of these irradiance/nutrient features would thus apparently be necessary to simulate these interactions numerically.

Second, unlike other similar studies (e.g. Heinle et al. 1979), we purposely excluded larger grazers by filtration to focus on the response of phytoplankton and not on algal growth – grazing relationships. Some protozoan grazers can pass through the filters we used; these grazers are known to play an important role in nutrient cycling in Chesapeake Bay (Correll et al. 1975) and have caused the catastrophic collapse of phytoplanktonic biomass in other large-scale enrichment experiments (D'Elia et al. 1977), but were not abundant enough in our experiments to be a significant source of grazing pressure.

Finally, although nutrient recycling by zooplankton grazing in the water column must be an essential feature of the natural environment, such in situ recycling *cannot* increase the standing stocks of organic matter that are ultimately controlled by nutrient concentrations. It is often misunderstood that although in situ nutrient cycling can enhance the rate of primary productivity, *the maximum standing stock of phytoplankton that can be reached is ultimately limited by the growth characteristics and nutrient requirements of the algae*, not the rate of recycling.

Methodological Considerations

A critical feature of our approach is excellent replicability. Other investigations of algal response to pollutant additions have used the same systems; each required good replicability to separate natural from experimental variability (Sanders et al. 1981; Sanders and Vermersch 1982; Sanders and Cibik 1985). The replicability of the rapid initial growth response suggests that we can extrapolate nutrient enrichment effects in the tanks to in the field. Nonetheless, the enhancement of phytoplankton growth in our cultures can only represent a nutrient's "algal growth-stimulation potential," and the intact ecological system may respond differently to enrichment than do its primary producers alone.

Of the typical concerns about "enclosure" studies, "chamber" and "wall" effects inevitably come to mind. Growth of bacteria, epiphytes, etc., on the walls of the tanks has been negligible in the first 2 wk of an experiment, when we place greatest confidence in the results.

The dilution rate of the culture is an important variable to consider also. According to continuous culture theory (cf. Goldman 1979a), steady-state biomass concentrations in the tank would imply growth rates of phytoplankton equal to the dilution rate, and increases and decreases in biomass with time imply transient growth rates greater and less than the $0.5 \cdot d^{-1}$ dilution rate we used. The close comparison between the changes of biomass in the river and in the tanks during some experiments suggests that the growth rates and dispersive removal of phytoplankton in the river must closely approximate the growth and dilution rates in the culture.

Management Implications

During the late summer the Chesapeake and its tributary estuaries exhibit maximum dissolved oxygen deficits (Taft et al. 1980; Officer et al. 1984). Nutrient enrichment is believed to be exacerbating these deficits by increasing the amount of organic matter present. In the Patuxent estuary, the deficits occur in the seaward 40 km (Heinle et al. 1980) when deposition of organic matter to the sediments is most intense (Kemp and Boynton 1984). A simple calculation serves to relate the biomass levels we obtained to potential oxygen demand: the maximum level reported was approximately 70 μg chlorophyll $a \cdot L^{-1}$, which is equivalent to ~2.1 mg organic material $\cdot L^{-1}$ (Strickland 1960), and represents a potential oxygen demand of about 7.5 mg $\cdot L^{-1}$ (cf. Price et al. 1985, table 1). At typical summer temperatures, the potential oxygen demand this biomass alone represents is sufficient to cause even fully saturated estuarine water to become anoxic.

As Ryther and Dunstan (1971) have noted, N:P ratios in both coastal waters and domestic wastewater are usually lower than in marine phytoplankton. Thus, P supplies in these waters appear to exceed phytoplanktonic demand. Additional evidence from other estuarine areas suggests that accelerated release of P from the sediments maintains elevated concentrations in the water column, particularly during the warmer months (e.g. Pomeroy et al. 1972; Pilson et al. 1980). Similar reasoning and our present data suggest that preventing future additions of N to the mesohaline region of the estuary will be necessary if autochthonous organic production must be controlled in the summer — providing it is also determined that residual oxygen demand from productivity in preceding seasons is not itself the cause of the oxygen deficits. Given the interannual variation in phytoplanktonic response to enrichment, a seasonal strategy to manage nutrient inputs may be a reasonable alternative if expensive treatment processes are required. However, before seasonal strategies are implemented, the lag time between the production of algal biomass and its decay must be determined.

Many management strategies affecting coastal water bodies are developed using dynamic "water-quality" models which, in turn, are largely based on experience gained from field studies of riverine and lacustrine phytoplankton dynamics. Differences between freshwater and estuarine systems may prevent the direct transfer of models from one system type to another. While studies like ours cannot supplant the use of water-quality models in the management process, they can be useful in the calibration and verification process. For example, the approach used here potentially yields information on seasonal variations in nutrient limitation, responses and species succession of natural phytoplankton species to nutrient enrichment, maximum growth rates of natural phytoplankton species, phytoplanktonic nutrient preferences, and biomass yields with given enrichments.

A study that focuses on the responses of a phytoplankton community in "microcosm" cannot be expected to reproduce all aspects of response of the real environment to nutrient addition. Nonetheless, such experimental "microcosms" or "mesocosms" are tools in understanding ecological processes relevant to management needs (Odum 1984; Pritchard and Bourquin 1984).

Acknowledgments

We thank Mr. S. Cibik and Ms. L. Currence for the operation and maintenance of the large-volume cultures, Mr. E. Roden for data management, Ms. C. Keefe and Ms. K. Wood for technical assistance, Ms. F. Younger for doing figures, Mr. J. Love for editorial assistance, and Ms. S. Ferguson and Ms. G. Canaday for help with manuscript preparation. Drs. S. Tarapchak, R. Magnien, and K. Tenore made many useful comments on the manuscript. This research was supported by the Office of Environmental Programs, Department of Health and Mental Hygiene, State of Maryland; the Maryland Water Resources Research Center; the Maryland Sea Grant Program; Procter and Gamble; and FMC Corporation.

References

BISHOP, S. S., K. A. EMMANUELE, AND J. A. YODER. 1984. Nutrient limitation of phytoplankton growth in Georgia nearshore waters. Estuaries 7: 506–512.

BOYNTON, W. R., W. M. KEMP, AND C. W. KEEFE. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production, p. 69–90. *In* V. Kennedy [ed.] Estuarine comparisons. Academic Press, New York, NY.

BRUSH, G. S. 1984. Stratigraphic evidence of eutrophication in an estuary. Water Res. 20: 531–541.

CORRELL, D. L., M. A. FAUST, AND D. J. SEVERN. 1975. Phosphorus flux and cycling in estuaries, p. 108–136. *In* L. E. Cronin [ed.] Estuarine research. Vol. 1. Chemistry, biology and the estuarine system. Academic Press, New York, NY.

D'ELIA, C. F., J. H. RYTHER, AND T. M. LOSORDO. 1977. Productivity and nitrogen balance in large-scale phytoplankton cultures. Water Res. 11: 1031–1040.

GOLDMAN, J. C. 1979a. Outdoor algal mass cultures. I. Applications. Water Res. 13: 1–19.

1979b. Outdoor algal mass cultures. II. Photosynthetic yield limitations. Water Res. 13: 119–136.

GOLDMAN, J. C., AND J. H. RYTHER. 1975. Nutrient transformations in mass cultures of marine algae. ASCE J. Environ. Eng. Div. 101: 351–364.

GOLDMAN, J. C., K. R. TENORE, AND H. I. STANLEY. 1973. Inorganic nitrogen removal from wastewater: effect on phytoplankton growth in coastal marine waters. Science (Wash., DC) 180: 955–956.

GRAY, J. S., AND E. PAASCHE. 1984. On marine eutrophication. Mar. Pollut. Bull. 15: 349–350.

HEINLE, D. R., C. F. D'ELIA, J. L. TAFT, J. S. WILSON, M. COLE-JONES, A. B. CAPLINS, AND L. E. CRONIN. 1980. Historical review of water quality and climatic data from Chesapeake Bay with emphasis on effects of enrichment. USEPA Chesapeake Bay Program Final Report, Grant No. R806189010. Chesapeake Research Consortium, Inc. Publ. No. 84, Annapolis, MD. Rep. No. TR-002E. UMCEES 80-15CBL.

HEINLE, D. R., D. A. FLEMER, R. T. HUFF, S. T. SULKIN, AND R. E. ULANOWICZ. 1979. Effects of perturbations on estuarine microcosms, p. 119–141. *In* R. F. Dame [ed.] Marsh–estuarine systems simulation. University of South Carolina Press, Columbia, SC.

JAWORSKI, N. A. 1981. Sources of nutrients and the scale of eutrophication problems in estuaries, p. 83–110. *In* B. J. Neilson and L. E. Cronin [ed.] Estuaries and nutrients. Humana Press, Clifton, NJ.

JAWORSKI, N. A., D. W. LEAR, JR., AND O. VILLA, JR. 1972. Nutrient management in the Potomac estuary, p. 246–272. *In* G. E. Likens [ed.] Nutrients and eutrophication. Am. Soc. Limnol. Oceanogr. Spec. Symp. Vol. 1, Lawrence, KS.

KEEFE, C. W., D. A. FLEMER, AND D. H. HAMILTON. 1976. Seston distribution in the Patuxent River Estuary. Chesapeake Sci. 17: 56–59.

KEMP, W. M., AND W. R. BOYNTON. 1984. Spatial and temporal coupling of nutrient inputs to estuarine primary production: the role of particulate transport and decomposition. Bull. Mar. Sci. 35: 522–535.

LIN, C. K., AND C. L. SCHELSKE. 1981. Seasonal variation of potential nutrient limitation to chlorophyll production in southern Lake Huron. Can. J. Fish. Aquat. Sci. 38: 1–9.

MAESTRINI, S. Y., D. J. BONIN, AND M. R. DROOP. 1984a. Phytoplankton as indicators of sea water quality: bioassay approach and protocols, p. 71–132. *In* L. E. Shubert [ed.] Algae as ecological indicators. Academic Press, New York, NY.

MAESTRINI, S. Y., M. R. DROOP, AND D. J. BONIN. 1984b. Test algae as indicators of sea water quality: prospects, p. 133–188. *In* L. E. Shubert [ed.] Algae as ecological indicators. Academic Press, New York, NY.

O'CONNOR, D. J. 1981. Modeling of eutrophication in estuaries, p. 183–223. *In* B. J. Neilson and L. E. Cronin [ed.] Estuaries and nutrients. Humana Press, Clifton, NJ.

O'CONNOR, D. J., R. V. THOMANN, AND D. M. DITORO. 1977. Water-quality analysis of estuarine systems, p. 71–83. *In* Estuaries, geophysics, and the environment. National Aademy of Sciences, Washington, DC.

ODUM, E. P. 1984. The mesocosm. BioScience 34: 558–562.

OFFICE OF ENVIRONMENTAL PROGRAMS. 1982. Nutrient control strategy for the Patuxent River basin. Department of Health and Mental Hygiene, State of Maryland. 52 p.

OFFICER, C. B., R. B. BIGGS, J. TAFT, L. E. CRONIN, M. A. TYLER, AND W. R. BOYNTON. 1984. Chesapeake Bay anoxia: origin, development, and significance. Science (Wash., DC) 223: 22–27.

PILSON, M. E. Q., C. A. OVIATT, AND S. W. NIXON. 1980. Annual nutrient cycles in a marine microcosm, p. 753–778. *In* J. P. Giesy [ed.] Microcosms in ecological research. DOE Symposium Series, Augusta, Georgia, Nov. 8–10, 1978, CONF 781101, NTIS.

POMEROY, L. R., L. R. SHENTON, R. D. H. JONES, AND R. J. REIMHOLD. 1972. Nutrient flux in estuaries, p. 274–291. *In* G. E. Likens [ed.] Nutrients and eutrophication. Am. Soc. Limnol. Oceanogr. Spec. Symp. Vol. 1, Lawrence, KS.

PRICE, K. S., D. A. FLEMER, J. L. TAFT, G. B. MACKIERNAN, W. NEHLSEN, R. B. BIGGS, N. H. BURGER, AND D. A. BLAYLOCK. 1985. Nutrient enrichment of Chesapeake Bay and its impact on the habitat of striped bass: a speculative hypothesis. Trans. Am. Fish. Soc. 114: 97–106.

PRITCHARD, D. W. 1955. Estuarine circulation patterns. Proc. Am. Soc. Civ. Eng. 81: 1–11.

PRITCHARD, P. H., AND A. W. BOURQUIN. 1984. The use of microcosms for evaluation of interactions between pollutants and microorganisms, p. 133–215. *In* C. C. Marshall [ed.] Advances in microbial ecology. Vol. 7. Plenum Press, New York, NY.

REDFIELD, A. C. 1934. On the proportions of organic derivatives in seawater and their relation to the composition of the plankton, p. 176–192. *In* James Johnstone Memorial Volume. Liverpool University Press, Liverpool.

RYTHER, J. H., AND W. M. DUNSTAN. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science (Wash., DC) 171: 1008–1013.

SANDERS, J. G., AND S. J. CIBIK. 1985. Adaptive behavior of euryhaline phytoplankton communities to arsenic stress. Mar. Ecol. Prog. Ser. 24: 199–205.

SANDERS, J. G., J. H. RYTHER, AND J. H. BATCHELDER. 1981. Effects of copper, chlorine, and thermal addition on the species composition of marine phytoplankton. J. Exp. Mar. Biol. Ecol. 49: 81–102.

SANDERS, J. G., AND P. S. VERMERSCH. 1982. Response of marine phytoplankton to low levels of arsenate. J. Plankton Res. 4: 881–893.

SCHELSKE, C. L. 1984. *In situ* and natural phytoplankton assemblages bioassays, p. 15–47. *In* L. E. Shubert [ed.] Algae as ecological indicators. Academic Press, New York, NY.

SCHELSKE, C. L., M. S. SIMMONS, AND L. E. FELDT. 1975. Phytoplankton responses to phosphorus and silica enrichments in Lake Michigan. Verh. Int. Ver. Limnol. 19: 911–921.

SCHELSKE, C. L., AND E. F. STOERMER. 1972. Phosphorus, silica and eutrophication of Lake Michigan, p. 157–171. *In* G. E. Likens [ed.] Nutrients and eutrophication: the limiting nutrient controversy. Am. Soc. Limnol. Oceanogr. Spec. Symp. Vol. 1. Lawrence, KS.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

1981. Studies of eutrophication in lakes and their relevance to the estuarine environment, p. 71–82. *In* B. J. Neilson and L. E. Cronin [ed.] Estuaries and nutrients. Humana Press, Clifton, NJ.

SCHINDLER, D. W., AND E. J. FEE. 1974. Experimental Lakes area: whole-lake experiments in eutrophication. J. Fish. Res. Board Can. 31: 937–953.

SMAYDA, T. J. 1974. Bioassay of the growth potential of the surface water of lower Narragansett Bay over an annual cycle using the diatom *Thalassiosira pseudonana* (oceanic clone, 13-1). Limnol. Oceanogr. 19: 889–901.

STRICKLAND, J. D. H. 1960. Measuring the production of marine phytoplankton. Bull. Fish. Res. Board Can. 122: 172 p.

TAFT, J. L., AND W. R. TAYLOR. 1976. Phosphorus dynamics in some coastal plain estuaries, p. 79–89. *In* M. L. Wiley [ed.] Estuarine processes. Vol. 1. Academic Press, New York, NY.

TAFT, J. L., W. R. TAYLOR, E. O. HARTWIG, AND R. LOFTUS. 1980. Seasonal oxygen depletion in Chesapeake Bay. Estuaries 3: 242–247.

THOMAS, W. H., D. L. R. SEIBERT, AND A. N. DODSON. 1974. Phytoplankton enrichment experiments and bioassays in natural coastal seawater and in sewage outfall receiving waters off southern California. Estuarine Coastal Mar. Sci. 2: 191–206.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372.

U.S. ENVIRONMENTAL PROTECTION AGENCY. 1979. Methods for chemical analysis of water and wastes. Off. Res. Dev., Cincinnati, OH. EPA-600/4-79-020.

UTERMÖHL, H. 1958. Zur Vervollkommung der Quantitativen Phytoplankton-Methodik. Mitt. Int. Ver. Theor. Angew. Limnol. 9: 1–38.

VOLLENWEIDER, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. 33: 53–83.

WEBB, K. L., AND C. F. D'ELIA. 1980. Nutrient and oxygen redistribution during a spring/neap tidal cycle in a temperate estuary. Science (Wash., DC) 207: 983–985.

Phosphorus Enrichment, Silica Utilization, and Biogeochemical Silica Depletion in the Great Lakes[1,2]

Claire L. Schelske,[3,4] Eugene F. Stoermer,[3] Gary L. Fahnenstiel,[3,5] and Mark Haibach[4]

Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA

Schelske, C. L., E. F. Stoermer, G. L. Fahnenstiel, and M. Haibach, 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. 43: 407–415.

Our hypothesis that silica (Si) depletion in Lake Michigan and the severe Si depletion that characterizes the lower Great Lakes were induced by increased phosphorus (P) inputs was supported by bioassay experiments showing increased Si uptake by diatoms with relatively small P enrichments. We propose that severe Si depletion (Si concentrations being reduced to ≤ 0.39 mg $SiO_2 \cdot L^{-1}$ prior to thermal stratification) results when P levels are increased to the extent that increased diatom production reduces Si concentrations to limiting levels during the thermally mixed period. Large P enrichments such as those that characterized the eastern and central basis of Lake Erie and Lake Ontario in the early 1970s are necessary to produce severe Si depletion. It is clear that severe Si depletion in the lower lakes was produced by P enrichment because inflowing waters from Lake Huron have smaller P concentrations and larger Si concentrations than the outflowing waters of either Lake Erie or Lake Ontario. Severe Si depletion probably began in the 1940s or 1950s as the result of increased P loads from expanded sewering of an increasing urban population and the introduction of phosphate detergents. The model proposed for biogeochemical Si depletion is consistent with previous findings of high rates of internal recycling because, under steady-state conditions for Si inputs, any increase in diatom production will produce an increase in permanent sedimentation of biogenic Si provided some fraction of the increased biogenic Si production is not recycled or unless there is a compensating increase in dissolution of diatoms.

Notre hypothèse voulant que l'appauvrissement en silice (Si) du lac Michigan et celui très marqué des Grands lacs d'aval aient été provoqués par une augmentation des apports de phosphore (P) a été confirmée par des essais biologiques montrant qu'un enrichissement relativement faible en phosphore entraînerait une augmentation de l'assimilation de la Si par les diatomées. Nous formulons l'hypothèse qu'il y a appauvrissement très important en Si (teneur en Si $\leq$ 0,39 mg $SiO_2 \cdot L^{-1}$ avant la stratification thermique) quand les teneurs en P augmentent suffisamment pour que la production accrue de diatomées réduise la teneur en Si aux niveaux limitatifs pendant la période de mélange thermique. D'importants enrichissements en P, de l'ordre de ceux qui ont caractérisé les bassins est et central des lacs Érié et Ontario au début des années 70, sont nécessaires pour provoquer un épuisement poussé du Si. Il apparaît clairement que l'épuisement poussé du Si des lacs d'aval a été causé par l'enrichissement en P car les eaux provenant du lac Huron présentent des teneurs en P moins élevées et des teneurs en Si plus élevées que celles s'écoulant des lacs Érié et Ontario. Cet épuisement du Si a probablement débuté au cours des années 40 et 50 suite à l'augmentation des rejets de phosphore causée par la hausse du volume des eaux usées qui a accompagné la croissance des centres urbains, et suite à l'arrivée sur le marché des détersifs au phosphate. Le modèle proposé pour l'épuisement biogéochimique du Si est cohérent avec la découverte antérieure de taux élevés de recyclage interne car, en conditions d'équilibre pour les apports de Si, toute augmentation de la production de diatomées se traduit par une hausse de la sédimentation permanente du Si biogène, à condition qu'une certaine partie de la production accrue de ce Si ne soit pas recyclée ou à moins qu'il y ait compensation par une plus grande dissolution des diatomées.

Received November 19, 1984
Accepted May 17, 1985
(J8019)

Reçu le 19 novembre 1984
Accepté le 17 mai 1985

[1]This paper was presented at the P–Plankton Dynamics Symposium at the 27th Conference on Great Lakes Research, International Association for Great Lakes Research, Brock University, St. Catharines, Ont., May 1984.

[2]Contribution No. 416 of the Great Lakes Research Division, University of Michigan, and Contribution No. 446 at the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor.

[3]Also School of Natural Resources, University of Michigan.

[4]Also Department of Atmospheric and Oceanic Science, University of Michigan.

[5]Also Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor.

It is well known that nutrient enrichment, particularly phosphorus (P) enrichment, affects silica (Si) uptake by diatoms. Seasonal Si uptake by diatoms is well known from the classical studies of the English Lake District (see Reynolds 1984). It also has been suggested by Kilham (1971) that Si demand could be used as an index of environmental enrichment. Schelske (1975) proposed that areal Si and nitrate uptake could be used to assess trophic state in the upper Great Lakes, and Dobson et al. (1974) compiled data based on seasonal changes in Si and nitrate concentrations in the Great Lakes that were consistent with this concept. Previous studies

TABLE 1. Conditions in laboratory nutrient enrichment experiments on the P effects of additions on Si uptake.

Experiment type	P added ($\mu g \cdot L^{-1}$)	SiO_2 ($mg \cdot L^{-1}$)	NO_3-N ($mg \cdot L^{-1}$)	Light: Intensity ($\mu Ein \cdot m^{-2} \cdot s^{-1}$)	Light: L:D	Temp. (°C)
Spike[a]	0,1,3,5,10,20,40	0.56	0.170	85	12:12	11
	0,1,3,5,10,20,40[e]	1.90	0.270			
Factorial	5,15,25,40,60	0.74	0.23,0.84,1.12	~140	12:12	8–9
fixed level 1971[b]	60[e]	0.74	1.12			
Fixed	0,10	2.0	0.20	90	14:10	7
level 1980[c]	10[f]	2.0	0.20			
Semicontinuous[d]	$1.0 \cdot d^{-1}$	$0.056 \cdot d^{-1}$		5–115	16:8	6

[a]Initial Si and NO_3 conditions.
[b]Levels of total soluble P, Si, and NO_3-N that were maintained by nutrient additions during the experiment.
[c]Levels of soluble reactive P, Si, and NO_3 that were maintained by nutrient additions during the experiment.
[d]Daily replacement rate of 0.05; the complete treatment (Com) included vitamins, trace metals, and a chelating agent (see footnote e).
[e]Initial treatment included spikes of Fe (10 $\mu g \cdot L^{-1}$), Mn (1.0 $\mu g \cdot L^{-1}$), Mo (1.0 $\mu g \cdot L^{-1}$), Co (1.0 $\mu g \cdot L^{-1}$), EDTA (100 $\mu g \cdot L^{-1}$), biotin (0.01 $\mu g \cdot L^{-1}$), cobalamim (0.01 $\mu g \cdot L^{-1}$), and thiamine (0.13 $\mu g \cdot L^{-1}$).
[f]EDTA (1.2 $\mu mol \cdot L^{-1}$) was added as a spike at the beginning of the experiment.

of the Great Lakes showed that Si uptake or utilization was correlated with total phosphorus (TP) concentrations only in the three upper Great Lakes, but not in Lake Erie and Lake Ontario. Here we present a new analysis of effects of P loading on Si dynamics in waters of the Great Lakes and, with the support of data from nutrient enrichment experiments, propose a new Si depletion model for all the Great Lakes.

Several terms must be defined, including distinguishing Si depletion from Si utilization or uptake by diatoms. Si depletion will be used to refer to the relatively long-term biogeochemical decrease in Si concentrations that has been postulated for Lake Michigan (Schelske and Stoermer 1971). Biogeochemical Si depletion, therefore, refers to decreases in Si concentrations in the water mass over periods of years or decades. Si utilization or uptake is the Si that disappears from the water column on an annual basis as the result of biogenic Si production by diatoms. Here, Si is used to designate SiO_2 and severe Si limitation will be defined to have occurred when the ambient SiO_2 concentration is ≤ 0.39 mg $\cdot L^{-1}$. This concentration has been proposed as K_{lim} (Si concentration where the diatom growth rate $\mu = 0.90\ \mu_{max}$) by Parker et al. (1977a) for Lake Michigan and was based on laboratory studies by Kilham (1975) of Si uptake by a clone of *Asterionella formosa* isolated from Lake Windemere. Subsequent studies have shown that K_{lim} for many species would be >0.40 mg $SiO_2 \cdot L^{-1}$ (Tilman et al. 1982). Thus, many diatom populations may be severely Si limited at concentrations >0.40 mg $SiO_2 \cdot L^{-1}$, especially at summer epilimnetic temperatures (see Lin and Schelske 1978).

Large increases in Si uptake by diatoms as the result of P enrichment have been demonstrated previously in studies of the Great Lakes except Lake Superior. Si uptake increased with P enrichment of Lake Michigan waters in laboratory (Schelske et al. 1984a) and in situ bag and bottle experiments (Schelske and Stoermer 1972; Schelske et al. 1975) and with P enrichment of Lake Huron waters in laboratory experiments (Lin and Schelske 1978). Levels of P in western Lake Erie waters were large enough naturally to produce large rates of Si uptake in laboratory experiments (Hartig 1985) with or without experimental enrichment. In Lake Superior, P enrichment increased the growth rate of the oligotrophic *Cyclotella* assemblage severalfold, but the resulting increase in standing crop of these nanoplanktonic populations resulted in a very small Si demand for diatom production compared with that found in other Great Lakes experiments (Schelske et al. 1972).

We address two questions: How much can the rate of Si utilization by diatoms in the Great Lakes be affected by P enrichment? What mechanism(s) have produced the severe Si depletion that characterizes the entire water column in Lake Ontario and the eastern and central basins of Lake Erie? In these lakes the annual range in concentrations is <0.1 to 0.5 mg $SiO_2 \cdot L^{-1}$ (Dobson et al. 1974).

In discussions of effects of P enrichment on Si depletion it is assumed that a small but unknown fraction of the diatoms that are produced will be permanently buried. This assumption can be justified with simple mass balance calculations (Schelske 1985) and is consistent with previous conclusions by Parker et al. (1977b) that possibly as little as 5% of the biogenic Si produced by diatoms is permanently buried and that internal recycling is the main source of Si for diatom production (Conway et al. 1977).

Methods

Four sets of laboratory experiments with natural phytoplankton assemblages in water collected from Lake Michigan were used to determine Si uptake rates under different P, other nutrient, and light conditions. Similar experiments have been conducted in our laboratory previously, but Si uptake rates have only been reported from two of these (Lin and Schelske 1978; Schelske et al. 1984a). Three types of nutrient additions were used: fixed level, semicontinuous, and spike (Table 1). Nutrients were measured with an autoanalyzer system, and chlorophyll *a* was determined fluorometrically on samples extracted with 90% acetone. Water for the factorial fixed level experiment was collected 9 November 1971 from a dock at Traverse City, Michigan, at the south end of the west arm of Grand Traverse Bay. Water for the April 1980 fixed level experiment was collected 11 km offshore from the Donald C. Cook Nuclear Power Plant, Bridgman, Michigan. Water for the semicontinuous and 15 October 1978 spike experiments

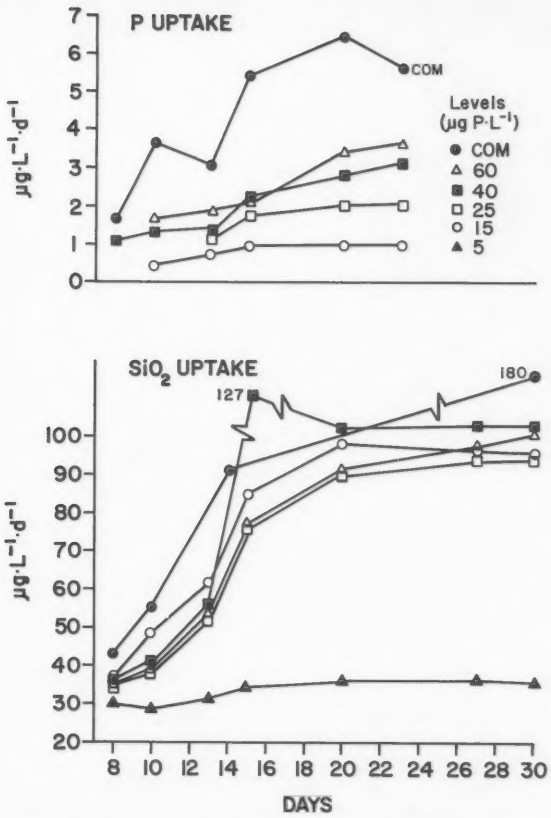


FIG. 1. P and Si uptake in the factorial fixed level experiment. Uptake rates for days designated are based on additions required to maintain fixed levels shown in Table 1. Uptake rates for P at the P1 level were not calculated because only 0.43 μg P·L^{-1} was added in total to the three treatments at this level.

was collected 25 and 10 km west of Grand Haven, Michigan.

The 1971 fixed level experiment employed a factorial design with five levels of P and three levels of nitrate nitrogen (N), which along with Si were maintained during the experiment at the levels designated in Table 1. In addition to the 15 combinations of P and N, a complete treatment (Com) was used which consisted of the highest N and P level plus additions of vitamins, trace metals, and a chelating agent at the beginning of the experiment. Effects of these treatments on community and population dynamics have been reported previously (Schelske et al. 1974; Stoermer et al. 1978). Because N effects were small, data for the three levels of N enrichment at each P level were averaged. These experiments were run in 20-L translucent plastic containers. In the 1980 fixed level experiment, P, N, and Si were maintained at fixed levels in 500-mL polycarbonate flasks.

The semicontinuous experiments were run in 500-mL clear polycarbonate Erlenmeyer flasks with 10% of the volume being replaced every 2 d with lake water that had been filtered through a 0.22-μm filter. Nutrients also were added at these 2-d intervals during the 29-d experiment (Table 1). Si and soluble reactive P concentrations on which rates of uptake were based were determined only at the end of the experiment. Phytoplankton biomass was determined with species abundance and volume data using a specific density of 1 (Fahnenstiel et al. 1984). Results of treatments on community phytoplankton dynamics have been reported (Fahnenstiel et al. 1984).

Spike experiments with the nutrient treatment shown in Table 1 were run in duplicate in 500-mL clear polycarbonate Erlenmeyer flasks. Nutrients were added only at the beginning of the experiment, while Si and N concentrations were measured seven times during the experiment.

Areal Si utilization (SU) was calculated for Lake Superior, Lake Huron, and Lake Ontario using data given in Dobson et al. (1974) and for Lake Michigan using data reported by Rousar (1973) and Schelske et al. (1984b). Equation 1 yields data for the thermally mixed and summer stratified periods (Schelske et al. 1984b):

$$(1)\quad SU = Z_m(C_{wm} - C_{sc}) + Z_t(C_{sc} - C_{sm})$$

where Z_m = average water depth (metres), Z_t = trophogenic zone depth (metres), C_{wm} = winter maximum concentration (grams per cubic metre), C_{sc} = minimum spring circulation concentration (grams per cubic metre), and C_{sm} = minimum summer trophogenic zone concentration (grams per cubic metre). In the calculations reported here, Z_t for all lakes was assumed to be 40 m, which may overestimate the depth of the trophogenic zone in the lower Great Lakes.

Results

Si Uptake in Enrichment Experiments

Rates of P uptake in the factorial fixed level experiments increased with increasing P enrichment even though there was little difference in the rates of Si uptake among the four highest levels of P enrichment (Fig. 1). Si uptake after 30 d amounted to 1.07 mg·L^{-1} in the treatment without P enrichment. By comparison, Si uptake at 30 d was nearly three times greater at the 15–60 μg P·L^{-1} levels of P enrichment, ranging from 2.83 to 3.08 mg·L^{-1}, and was 5.4 mg·L^{-1} in the Com treatment. By day 20, Si uptake rates approached equilibrium values, which were 36 μg·L^{-1}·d^{-1} for the control P level and 93–100 μg·L^{-1}·d^{-1} for the remaining four levels of P enrichment (Fig. 1). In the Com treatment the maximum daily uptake rate was 180 μg·L^{-1}·d^{-1}. P uptake in the Com treatment was at least 50% greater than in the treatment that had the same level of P enrichment but no additions of vitamins, trace metals, and EDTA. Because of differences in uptake rates of P, Si:P atomic ratios varied greatly among the P treatments, ranging on day 20 from 74.4 at the lowest level to 13.9 at the highest level of P enrichment (Table 2). Calculated Si:P uptake ratios increased in all treatments from day 20 to 30, but these results are misleading because P was added at levels in excess of that required for growth and no P was added after day 20.

Si uptake in the April fixed level experiments also increased with added P, N, and Si. Si uptake in comparison with the control increased about 10-fold to 21 ± 5 μg·L^{-1}·d^{-1} with additions of P, N, and Si and about 15-fold in the treatment that included EDTA (Table 3). Increased uptake of Si in all treatments was reflected by increased uptake of P and by increased production of chlorophyll *a*. Si uptake rates in this experiment were smaller than in the factorial experiment because it was terminated at day 9 while the rate of production was still increasing and before uptake rates reached equilibrium values.

TABLE 2. Si:P uptake atomic ratios in the factorial fixed level experiment. Uptake based on Si and P additions required to maintain nutrient levels shown in Table 1. No data are calculated for measurements made after day 20 because this is the last day when levels for both nutrients were adjusted.

P ($\mu g \cdot L^{-1}$)	Day			
	10	13	15	20
5	—	—	—	74.4[a]
15	51.1	44.6	46.9	50.9
25	—	24.1	22.7	23.0
40	16.0	20.8	29.8	18.7
60	11.8	14.8	18.8	13.9
Com	7.9	15.6	34.6	21.7

[a]Ratio based on a hypothetical uptake of 5 $\mu g \ P \cdot L^{-1}$ or an amount equivalent to the measured level of total soluble P in this level of treatment (see Fig. 1).

TABLE 3. Rates of Si utilization, P uptake, and chlorophyll *a* production in Lake Michigan fixed level experiments, April 1980. Uptake rates ($\mu g \cdot L^{-1} \cdot d^{-1}$) are means ± standard deviations for three replicates ($N = 3$) based on a 9-d growth period.

Treatment	Uptake		Production, Chl *a*
	SiO_2	PO_4-P	
Control	2 ± 2	−0.15 ± 0.03	0.40 ± 0.04
P, N, SiO_2	21 ± 5	2.00 ± 0.04	0.78 ± 0.15
P, N, SiO_2, EDTA	34 ± 2	3.00 ± 0.06	1.56 ± 0.29

TABLE 4. Rates of Si utilization ($\mu g \ SiO_2 \cdot L^{-1} \cdot d^{-1}$) in October spike experiment. Uptake rates were calculated for a 15-d period unless noted otherwise.

P additions ($\mu g \cdot L^{-1}$)	Rate of Si utilization	
	Ambient Si	Com
0	16.0	19.3
1	25.7	37.1
3	31.1	64.2
5	34.2	95.6
10	37.1	141[a]
20	37.1	175[b]
40	37.1	183[b]

[a]13-d uptake period.
[b]10-d uptake period.

P additions in the October spike experiments caused Si depletion because Si supplies were not replenished. Si concentrations were reduced to K_{lim} (0.39 $mg \cdot L^{-1}$) in <10 d with P additions ranging from 5 to 20 $\mu g \cdot L^{-1}$ (Fig. 2). In the Com treatments with added Si, Si concentrations $< K_{lim}$ were obtained in <10 d only at the 20 and 40 $\mu g \cdot L^{-1}$ P enrichments; however, by day 15, Si concentrations were reduced to $< K_{lim}$ in all treatments except the 0−5 $\mu g \cdot L^{-1}$ P enrichments. Maximum Si uptake rates, averaged over the 15-d experiment, were 37 $\mu g \cdot L^{-1} \cdot d^{-1}$ for the 10−40 $\mu g \cdot L^{-1}$ P enrichments alone and 180 $\mu g \cdot L^{-1} \cdot d^{-1}$ over a 10-d period for the 20 and 40 $\mu g \cdot L^{-1}$ P Com enrichments with added Si (Table 4). These data show that Si uptake increased with P enrichment until

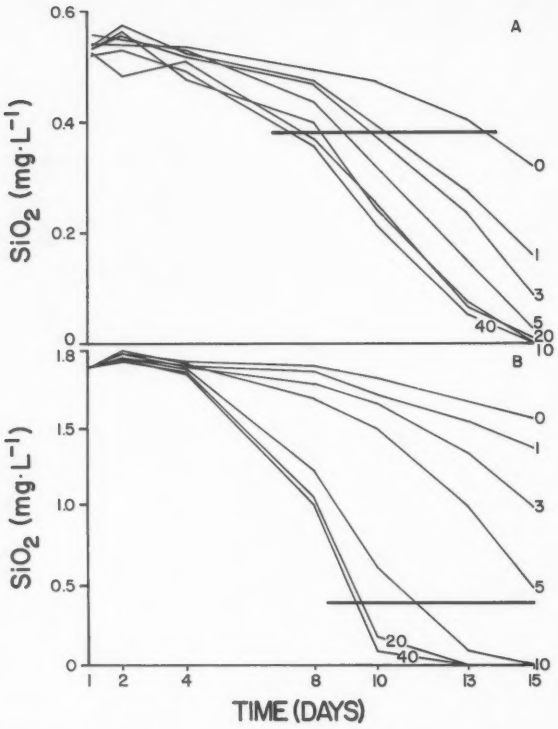


FIG. 2. Si uptake in the spike experiment during logarithmic growth (see Fig. 2). (A) Si uptake for P enrichments alone; (B) Si uptake for different P enrichments in a Complete (Com) treatment (see Table 1). The horizontal line designates K_{lim} (see text).

it was limited by Si supplies in treatments with or without added Si.

Effects of P and Si enrichment on Si uptake as a function of light intensity were determined in the semicontinuous experiments. The equilibrium concentration of Si was 1.1−1.2 $mg \cdot L^{-1}$ at the lowest light level in the SiO_2, SiO_2 + P, and Com treatments (Table 5). There was essentially no Si uptake in the SiO_2 treatment across light levels, presumably because there was little growth of the P-limited phytoplankton. At the end of this experiment, Si uptake in the two treatments with added P (SiO_2 + P and Com) was essentially equal to the supply rate of 56.8 $\mu g \cdot L^{-1} \cdot d^{-1}$, which is evident because Si concentrations at the highest light levels were reduced to <0.1 $mg \cdot L^{-1}$. Uptake rates equal to the supply rate were obtained in the Com and SiO_2 treatments at light levels as low as 15 and 25 $\mu Ein \cdot m^{-2} \cdot s^{-1}$ and at approximately half the supply rate at 8 and 15 $\mu Ein \cdot m^{-2} \cdot s^{-1}$, respectively.

Phytoplankton growth in all the nutrient enrichment experiments was P limited, and increased Si uptake resulting from P enrichment can be attributed to increased diatom production. Growth rates in the factorial fixed level experiment, as reported previously by Schelske et al. (1974), among the four highest P levels were not significantly different and were three times greater than in the control treatment. In the October spike experiments, standing crops, measured as chlorophyll *a*, increased with increasing P level but these increases were not proportional to P concentrations at the highest level of P enrich-

TABLE 5. Steady-state concentrations of soluble reactive P ($\mu g \cdot L^{-1}$) and Si (mg $SiO_2 \cdot L^{-1}$) at different light levels on day 29 of the semicontinuous experiment.

	Light level ($\mu Ein \cdot m^{-2} \cdot s^{-1}$)					
Treatment	5	8	15	25	50	115
Control						
P	0.2	0.8	0.65	0.4	0.4	1.1
SiO_2	0.15	0.15	0.1	0.11	0.3	0.1
SiO_2						
P	1.0	1.89	0.4	0.5	0.2	0.3
SiO_2	1.1	1.1	1.0	1.1	1.0	1.0
P						
P	7.94	0.3	0.5	0.12	0.36	0.2
SiO_2	0.12	0.07	0	0.02	0.09	0.05
SiO_2 + P						
P	7.88	0.83	0.6	0.77	1.1	0.7
SiO_2	1.16	0.9	0.45	0.08	0.08	0.11
Com						
P	4.35	0.7	0.4	0.6	0.4	0.4
SiO_2	1.07	0.44	0.01	0.01	0.01	0.05

ment (Fig. 3). Cessation of logarithmic growth in these experiments coincided with severe Si limitation (Fig. 2), indicating that these assemblages were dominated by diatoms. In the semicontinuous experiments phytoplankton assemblages also were P limited as shown by standing crop data in Table 6. In addition, there was a Si−P interaction because growth was greater in the SiO_2 + P treatment than in either treatment with SiO_2 or P alone. This result of secondary nutrient enrichment is not unexpected because the dominant phytoplankton were diatoms (Fahnenstiel et al. 1984). It also had been established previously that increased production of diatoms resulted from P enrichment in the fixed level factorial experiment (Stoermer et al. 1978).

Dynamics of Si Utilization

Areal Si disappearance for the thermally mixed and thermally stratified periods was calculated using data on seasonal changes in Si concentrations. If areal utilization for the two periods is combined, the total for Lake Michigan is about twice as large as that for Lake Ontario (Table 7). Areal Si disappearance in Lake Ontario is larger than would be expected from first inspection of data on the annual range in Si concentrations because a major fraction of the total pool of dissolved Si in the water mass is utilized for diatom production during the winter−spring mixing period (Fig. 4). By comparison, the fraction utilized in Lake Michigan during winter−spring mixing is much smaller, <30% of the winter maximum supply. According to data presented by Dobson et al. (1974), Si concentrations in Lake Ontario are <0.4 mg·L^{-1} for at least 8 mo of the year, being greater only from December through March, and the annual range in Si concentrations for the eastern and central basins of Lake Erie and Lake Ontario is only 0.3 mg·L^{-1}. In Lake Michigan, the annual range in Si concentration is 1.4 mg·L^{-1}. The amount of Si utilization in Lake Ontario, therefore, is less than that in Lake Michigan because the Si supply is smaller.

Phasing of areal Si utilization, which can be related to P enrichment, varies seasonally in the Great Lakes as shown in Fig. 4 and Table 7. In Lake Ontario, P supplies are large and

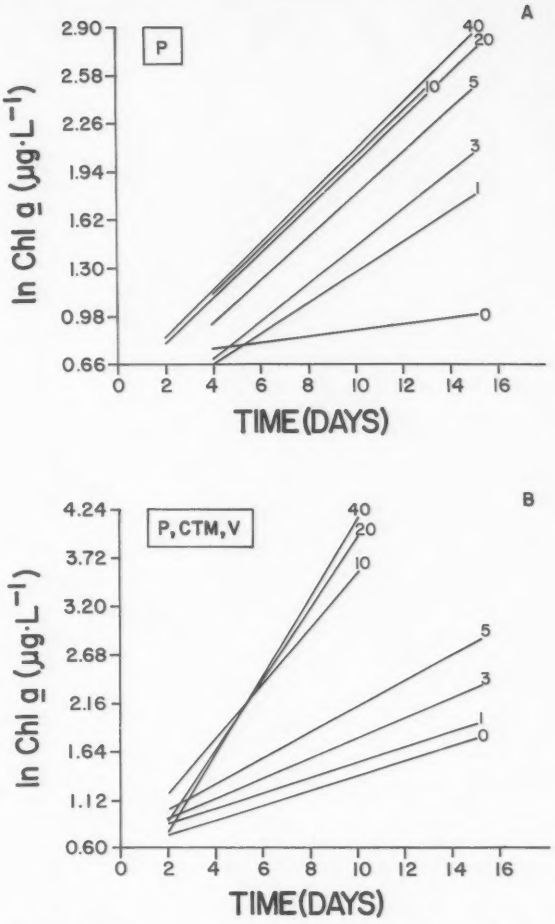


FIG. 3. Growth responses of phytoplankton assemblages in the spike experiment measured as chlorophyll *a* during period of logarithmic growth. (A) Growth responses for P enrichment alone; (B) growth responses for different P enrichment in a Complete (Com) treatment (see Table 1).

as a consequence the available reservoir of Si in the water column is mostly utilized before the water column is stratified thermally. In Lake Superior, thermal stratification is delayed because of the large average depth, and as a consequence, a significant fraction of the Si uptake occurs prior to thermal stratification even though P levels are low. Areal Si utilization in Lake Michigan is also divided about equally between the mixed period and the thermally stratified period; however, Si uptake in the stratified period is probably limited because Si supplies are depleted and diatom production is Si limited during part of the year. This relationship is evident from data for Lake Huron where the TP concentration is less but where areal Si utilization during the stratified period is about equal to that in Lake Michigan. Compared with Lake Michigan, Lake Huron exhibits relatively high areal Si utilization at a lower P level because epilimnetic Si supplies limit diatom growth in Lake Michigan during the stratified period.

It was shown previously that areal Si utilization and levels of

TABLE 6. Steady-state biomass and chlorophyll *a* concentrations on day 29 at different light levels of the semicontinuous experiments. BM is biomass in $\mu g \cdot L^{-1}$ and Chl is chlorophyll *a* in $\mu g \cdot L^{-1}$.

	Light level ($\mu Ein \cdot m^{-2} \cdot s^{-1}$)					
Treatment	5	8	15	25	50	115
Control						
BM	642	1172	740	650	540	501
Chl	2.0	1.7	2.0	1.2	1.16	1.3
SiO_2						
BM	1015	380	1286	800	1336	1392
Chl	1.76	1.48	2.56	1.6	2.5	1.9
P						
BM	452	830	1560	2447	1600	3118
Chl	2.5	3.5	6.9	6.9	5.0	4.8
SiO_2 + P						
BM	420	878	2795	3900	5890	5275
Chl	3.1	5.6	12.0	10.8	8.2	5.21
Com						
BM	810	3700	4470	5600	5200	7547
Chl	3.79	14.0	22.5	13.3	10.6	10.0

TABLE 7. Areal Si utilization in the Great Lakes during the winter–spring mixed and summer stratified periods. Data are the mean depth ($\bar{Z}$) and areal Si utilization ($g\ SiO_2 \cdot m^{-2}$) for each period. Also see Fig. 4 and Eq. 1.

Lake	$\bar{Z}$ (m)	Mixed period	Stratified period
Superior	148	8–15	4–8
Huron	53	16	30
Michigan	84	34	36
Ontario	86	25–34[a]	0–8[a]

[a]Data for the eastern and central basins of Lake Erie would be similar.

P enrichment were related in the upper Great Lakes (Schelske 1975). It seems obvious from the data presented in Fig. 4 that P enrichment has affected Si dynamics in the Great Lakes because the reserve of Si (the amount of Si remaining in the water column after the stratified period) is inversely related to P enrichment. Lake Superior, which has the smallest TP concentration (4 $\mu g \cdot L^{-1}$), has the largest Si reserve, and Lake Ontario, which has the largest TP concentration (25 $\mu g \cdot L^{-1}$), has the smallest Si reserve. Thus, comparing Si reserves and TP data illustrates the relative degree of Si depletion among the Great Lakes and also the effect of P enrichment on biogeochemical Si depletion in these lakes.

Discussion

Nutrient Enrichment and Si Utilization

Results of nutrient enrichment experiments described here clearly show that P enrichment stimulated Si uptake by diatoms under a wide range of light, temperature, and nutrient conditions. Si was utilized at the supply rate of 56 $\mu g \cdot L^{-1} \cdot d^{-1}$ and was therefore maintained at severely limiting levels in semicontinuous experiments at light intensities as low as 15 and 25 $\mu Ein \cdot m^{-2} \cdot s^{-1}$ when both P and Si were supplied with and without other nutrients at 6°C (Table 5). Lin and Schelske (1978) showed that light and temperature affected Si uptake in laboratory experiments with enriched (Com treatment) Lake Huron water collected 17 March 1976. At 5°C, Si uptake rates (averaging 34.4 $\mu g \cdot L^{-1} \cdot d^{-1}$) were not affected by light. However, Si uptake was greater at 10 and 18°C and increased with light level at both temperatures. At 18°C, Si uptake appeared to be light limited and increased from 59.8 $\mu g \cdot L^{-1} \cdot d^{-1}$ at 40 $\mu Ein \cdot m^{-2} \cdot s^{-1}$ to 236 $\mu g \cdot L^{-1} \cdot d^{-1}$ at 160 $\mu Ein \cdot m^{-2} \cdot s^{-1}$. These data at 18°C for a 13:11 light–dark cycle show that a large spike of P (39 $\mu g\ P \cdot L^{-1}$) produced a Si demand that was 30% greater than the maximum found in any of our experiments. The higher rate can be attributed to Lin and Schelske's experiments being run at a higher temperature than any of our experiments. However, Si limitation probably reduced Si uptake rates in all of the spike experiments with high P enrichments and in semicontinuous treatments in which Si was essentially depleted as an effect of P enrichment.

Results of control treatments show that the Si demand for diatom production at ambient P levels can be large under some conditions. Si uptake rates in the controls (no added P) varied greatly and ranged from as low as 2 $\mu g \cdot L^{-1} \cdot d^{-1}$ in the April fixed level experiments (Table 3) to 16–19 $\mu g \cdot L^{-1} \cdot d^{-1}$ in the spike experiments (Table 4) and to more than 30 $\mu g \cdot L^{-1} \cdot d^{-1}$ in the factorial fixed level experiments (Fig. 1). Low Si uptake rates were obtained in the April fixed level experiment because the experiment was terminated after 9 d and in the spike experiment because Si supplies limited diatom growth. In addition, a greater rate of uptake would be expected in the fixed level control because water samples were collected from a dock in Grand Traverse Bay where P concentrations were probably greater than those for the offshore water used for the other experiments. As a consequence, Si uptake was greatest in the factorial fixed level control. By comparison, Si uptake in spike experiments conducted by Hartig (1985) at 5°C with water from western Lake Erie, which would contain larger concentrations of P than Lake Michigan, averaged 60 $\mu g \cdot L^{-1} \cdot d^{-1}$ over a 10-d period and 91 $\mu g \cdot L^{-1} \cdot d^{-1}$ over a 5-d period in control treatments. These large rates of Si uptake, which were obtained without P enrichment, may be attributable partly to experimental conditions. Si uptake in containers may be large be-

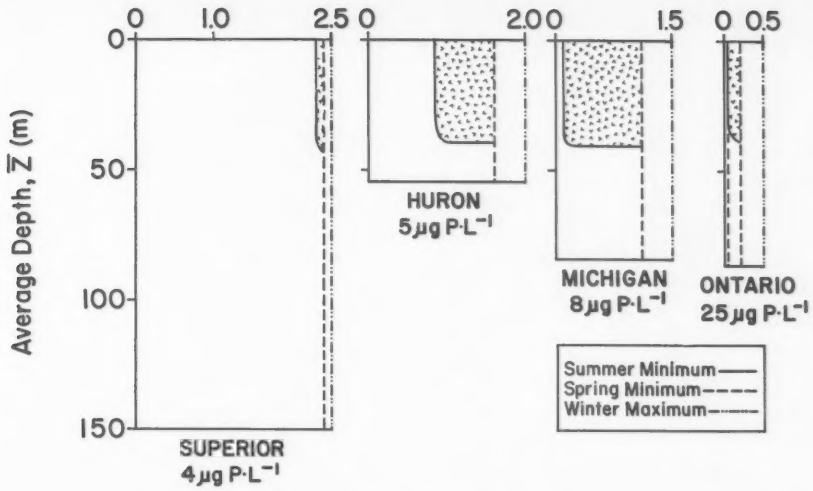


FIG. 4. Summer minimum, spring minimum, and winter maximum Si concentrations (mg $SiO_2 \cdot L^{-1}$) in the Great Lakes. Summer minimum is equivalent to the smallest epilimnetic concentration during summer stratification, spring minimum is the concentration at the initiation of thermal stratification, and winter maximum is the largest concentration during the winter–spring mixing period. Areal Si utilization is shown for the thermally stratified (stippled area) and winter mixed periods. P data shown for each lake are total P concentrations representative of the winter mixing period. Figure is based on data obtained from Dobson et al. (1974), Schelske et al. (1984b), and Rousar (1973). Although not shown, Si and TP data for the eastern and central basins of Lake Erie would be similar to those for Lake Ontario.

cause P is recycled more rapidly than Si. Although Si uptake rates reported are net uptake rates, Si uptake resulting from recycling is obviously negligible compared with that for P over the 9- to 30-d periods of these experiments.

We contend that severe Si limitation such as that found in the lower lakes is a consequence of increased P loading. Si uptake data from the spike experiments show that uptake rates increased rapidly with small P enrichments so that P enrichments of 1–3 $\mu g \cdot L^{-1}$ increased Si uptake two- to three-fold (Table 4). It therefore follows that P enrichment could in fact have had a profound effect on Si dynamics in Lake Michigan and the lower Great Lakes. Si uptake data obtained by Hartig (1985) confirm that the Si demand in the lower lakes is greater than in Lake Michigan. He found a 91 $\mu g \cdot L^{-1} \cdot d^{-1}$ rate of Si uptake averaged over a 5-d period at 60 and 120 $\mu Ein \cdot m^{-2} \cdot s^{-1}$ in experiments run at 5°C without P additions. His results confirm that ambient P levels in western Lake Erie are large enough to support high rates of Si uptake which can deplete Si supplies in a few days. The Si uptake rate of 36 $\mu g \cdot L^{-1} \cdot d^{-1}$ that occurred in the control P treatments of the factorial fixed level experiments (Fig. 1) provides a Si demand that is large enough to deplete the winter maximum Si concentration (1.4 $mg \cdot L^{-1}$) in Lake Michigan in 39 d. By contrast, this much Si would be utilized in 16 d at the uptake rate at 5°C obtained by Hartig (1985) in his control experiments. Thus, Si uptake data from nutrient enrichment experiments strongly support the hypothesis that increased diatom growth resulting from P enrichment could effectively utilize available Si supplies in Great Lakes waters within periods of days or weeks.

Data presented by Rousar (1973) show that after thermal stratification is established, about 1.0 mg $Si \cdot L^{-1}$ is utilized over a period of approximately 100 d in the epilimnetic waters of Lake Michigan. These data yield a crude Si uptake rate of approximately 10 $\mu g \cdot L^{-1} \cdot d^{-1}$ or about half that found in controls of the spike experiments. This is a net rate that does not account for regeneration of Si from diatoms nor for diffusion of Si from subsurface waters and thus is a conservative estimate of Si uptake and diatom production. If it is assumed that Si utilization is limited by and proportional to P supplies, then the threefold greater TP concentration in the lower lakes could produce a Si demand of 30 $\mu g \cdot L^{-1} \cdot d^{-1}$ or a rate of Si utilization over 9–11 d that is equivalent to the annual concentration range reported by Dobson et al. (1974) for the lower lakes.

Our nutrient experiment results demonstrate that relatively small P enrichments can increase diatom production several-fold. In addition, these results show experimentally that significant Si uptake could occur when light intensities are low, either at metalimnetic depths when Si is depleted in the epilimnion during summer stratification or during the winter mixed period when phytoplankton populations are light limited because the mixed depth is much greater than the compensation depth. Thus, one of the consequences of P enrichment is that increased diatom production causes a significant demand for Si during the winter mixed period. This, in turn, provides the mechanism by which severe Si depletion can occur throughout the water column early in the seasonal cycle in Lake Ontario and in the eastern and central basins of Lake Erie. Si uptake by diatoms in Lake Michigan is great enough to utilize approximately 0.4 $mg \cdot L^{-1}$ during the winter mixed period (see Schelske et al. 1984b). Levels of TP in the Great Lakes required to utilize and deplete Si supplied before the lake stratifies thermally therefore must lie somewhere between the TP level of approximately 8 $\mu g \cdot L^{-1}$ in Lake Michigan, which was associated with Si depletion in the early 1970s (Schelske et al. 1983), and the

25 μg $P \cdot L^{-1}$, which was found in Lake Ontario in the early 1970s during a clearly documented period of severe Si limitation (Dobson et al. 1974).

Biogeochemical Si Depletion

Comparing outflow losses of Si from Lake Superior and Lake Michigan with those from Lake Erie and Lake Ontario can be used to demonstrate that biogeochemical Si depletion is occurring presently in the Great Lakes as the result of P enrichment. Schelske (1985) reported that the combined outflow losses of Si from Lake Michigan and Lake Superior totalled 20×10^7 kg·yr^{-1}. However, the calculated annual outflow loss from Lake Erie or Lake Ontario is roughly 25% of that amount. This loss of 15×10^7 kg·yr^{-1} of Si that occurs after the outflows of Lake Michigan and Lake Superior enter Lake Huron can be attributed to permanent sediment of diatoms, primarily in the lower lakes. Relatively little Si has been lost when the water flows out of Lake Huron, which has a TP concentration of 5 μg·L^{-1} and ample Si supplies throughout the year (Fig. 4). In Lake Erie, however, waters are enriched with P, which in the early 1970s amounted to 29 μg·L^{-1} in the central basin of Lake Erie and 25 μg·L^{-1} in the eastern basin of Lake Erie and in Lake Ontario (Schelske et al. 1983). As a consequence of increased TP concentration, diatom production and sedimentation are increased and Si concentrations in the lower lakes are reduced drastically. The actual loss of Si to permanent sedimentation of diatoms in the lower lakes is much larger than 15×10^7 kg·yr^{-1} because to calculate the amount lost one must also consider all the inputs to Lake Huron and Lake Erie in addition to the inputs from Lake Michigan and Lake Superior.

The mechanism for biogeochemical Si depletion can be illustrated with the simple input−output mass balance equation (Eq. 2) in which the internal recycle terms are omitted (Schelske 1985):

$$(2) \quad TI + AI = OL + PS$$

where TI = tributary inputs, AI = atmospheric inputs, OL = outflow losses, and PS = permanent sedimentation. Permanent sedimentation is defined as the biogenic silica that is produced by diatoms and that is not dissolved either in the sediments or in the water column. Thus, from Eq. 2, if diatom production is increased and not all of the increased production is recycled, then the resulting increased permanent sedimentation of diatoms must produce biogeochemical Si depletion under steady-state conditions. This is true because, if permanent sedimentation increases, Si concentrations in the water mass and outflow losses also must decrease under steady-state conditions. Therefore, even if only 5% of the diatoms produced are permanently sedimented (Parker et al. 1977b), all of the increased diatom production that is permanently sedimented affects the steady-state mass balance, and biogeochemical Si depletion will result unless there is a compensating increase in dissolution rates of diatoms.

Four stages of Si limitation and types of Si dynamics can be identified and related to different levels of P enrichment in the Great Lakes (see Fig. 4). They are as follows in order of increasing TP concentrations.

(1) Small seasonal and annual changes in Si concentrations with little epilimnetic Si utilization (Lake Superior).

(2) Moderate seasonal and annual changes in Si concentrations with pronounced epilimnetic Si utilization during thermal stratification which is not great enough to limit diatom growth (Lake Huron).

(3) Maximum seasonal and annual changes in Si concentrations with the greatest seasonal change occurring in the epilimnion after thermal stratification. In this stage, diatom populations during late summer are severely Si limited in the epilimnion and probably also in the metalimnion (Lake Michigan). Larger seasonal changes undoubtedly characterized the annual Si cycle during the period of rapid biogeochemical Si depletion in Lake Michigan (see Schelske 1985).

(4) Moderate seasonal and annual changes in Si concentrations with the greatest change and severe Si depletion occurring before the water column is stratified thermally. In this stage, diatom populations are severely Si limited during most of the year. This stage can occur only when P supplies are great enough to produce water column Si depletion before the lake is stratified thermally (Lake Ontario and the eastern and central basins of Lake Erie).

It seems obvious that Lake Erie and Lake Ontario have progressed through all the stages of biogeochemical Si depletion as the result of historic increases in P loading. Based on paleolimnological evidence, epilimnetic Si depletion apparently occurred by the late 1800s in both of these lakes when P inputs increased as the result of forest clearance and early settlement in the drainage basin (Schelske et al. 1983). Severe Si depletion is a relatively recent occurrence, probably beginning in the 1940s or 1950s. In the sediment chronology for this period, Stoermer et al. (1985) found that the most abundant diatoms are benthic, nearshore, and stenothermal planktonic populations, which indicates that diatom production in response to Si limitation shifted from eurythermal offshore populations to populations that optimize Si supplies in the nearshore zone or in offshore waters prior to thermal stratification. In addition, there is evidence for increased deposition of biogenic Si during this period which must have occurred if Si supplies in the water mass were reduced in the 1940s or 1950s. Severe Si depletion therefore apparently has characterized Lake Ontario for more than 30 yr as a result of the combined effects of large increases in P loading that were associated with increased urban population growth and sewering and the introduction of phosphate detergents (Chapra 1977).

In summary, biogeochemical Si depletion in the Great Lakes therefore results from two processes related to imbalances between P and Si supplies. The first is the imbalance in P relative to Si in tributary inputs which was postulated by Schelske and Stoermer (1971). This imbalance occurs because some tributary inputs are enriched with P from domestic and agricultural sources (see Schelske 1975). The other imbalance that leads to Si depletion is the large difference in recycling rates of P and Si in the water column. Relatively rapid P turnover times are controlled primarily by biological processes and may have time constants of hours or days whereas dissolution of Si is a chemical process which has a much longer time constant and recycling is essentially an annual event that is controlled primarily by the annual thermal cycle.

Results of nutrient bioassay experiments supported the hypotheses that biogeochemical Si depletion resulted from increased P loading in the Great Lakes. We showed that small P enrichments stimulated diatom production and that increased diatom production can produce biogeochemical Si depletion provided all the increased diatom production is not recycled or there is not a compensating increase in the rate of recycling. These results are thus consistent with results of previous studies

that have shown high rates of internal recycling. Results of nutrient enrichment experiments also showed that Si uptake by diatoms could be increased with small P enrichments at low light and temperature, thus providing experimental evidence for significant Si uptake during the period of winter–spring convective mixing. To produce severe Si depletion, P supplies must be increased to the extent that Si uptake by diatoms can reduce Si supplies to limiting levels during this period. Thus, a mechanism is provided to explain the severe Si depletion (annual concentration range $<0.1-0.4$ or $0.5\ mg \cdot L^{-1}$) that presently characterizes Lake Ontario and the central and eastern basins of Lake Erie.

On the basis of results presented here, a conceptual model of biogeochemical silica depletion was developed that relates historic P loadings, changing seasonal Si demands for diatom production, and present Si concentrations in all the Great Lakes. The new model therefore is more comprehensive than the one proposed earlier which only related P enrichment and Si demand for the upper Great Lakes (Schelske 1975) and was not applicable to the lower Great Lakes where diatom growth is Si limited most of the year. The new model thus provides a mechanism to explain the severe type of Si depletion that occurred in Lake Ontario and the eastern and central basins of Lake Erie where, because of P enrichment, Si concentrations were probably reduced before the mid-1950s to levels that severely limited diatom growth most of the year.

Acknowledgments

We thank S. S. Kilham for reading the manuscript and providing helpful suggestions and S. J. Tarapchak for organizing the symposium and for encouraging and inviting the senior author to participate in the symposium. Data reported here were obtained with support from a previous contract with the U.S. Department of Energy (C00-2003-46) and a grant from the U.S. Environmental Protection Agency (R806294). The synthesis of data and preparation of this paper would not have been possible without current grants from the National Science Foundation (OCE-8216588) and the U.S. Environmental Protection Agency (R810396). We also wish to acknowledge partial travel support for the senior author to attend the symposium and publication costs that were provided by the Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI 48104.

References

CHAPRA, S. C. 1977. Total phosphorus model for the Great Lakes. J. Environ. Eng. Div. 103: 147–161.

CONWAY, H. L., J. I. PARKER, E. M. YAGUCHI, AND D. L. MELLINGER. 1977. Biological utilization and regeneration of silicon in Lake Michigan. J. Fish. Res. Board Can. 34: 537–544.

DOBSON, H. F. M., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in Lakes Erie, Huron and Superior. J. Fish. Res. Board Can. 31: 731–738.

FAHNENSTIEL, G. L., D. SCAVIA, AND C. L. SCHELSKE. 1984. Nutrient–light interactions in the Lake Michigan subsurface chlorophyll layer. Verh. Int. Ver. Limnol. 22: 440–444.

HARTIG, J. H. 1985. Factors contributing to the development of *Fragilaria crotonensis* Kitton "pulses" in the Pigeon Bay waters of western Lake Erie. Ph.D. thesis, University of Windsor, Windsor, Ont. 150 p.

KILHAM, P. 1971. A hypothesis concerning silica and the freshwater planktonic diatoms. Limnol. Oceanogr. 16: 10–18.

KILHAM, S. S. 1975. Kinetics of silicon-limited growth in the freshwater diatom *Asterionella formosa*. J. Phycol. 11: 396–399.

LIN, C. K., AND C. L. SCHELSKE. 1978. Effects of nutrient enrichment, light intensity and temperature on growth of phytoplankton from Lake Huron. Univ. Mich. Great Lakes Res. Div. Spec. Rep. 63: 61 p.

PARKER, J. I., H. L. CONWAY, AND E. M. YAGUCHI. 1977a. Seasonal periodicity of diatoms and silicon limitation in offshore Lake Michigan, 1975. J. Fish. Res. Board Can. 34: 552–558.

1977b. Dissolution of diatom frustules and recycling of amorphous silicon in Lake Michigan. J. Fish. Res. Board Can. 34: 545–551.

REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, New York, NY. 384 p.

ROUSAR, D. C. 1973. Seasonal and spatial changes in primary production and nutrients in Lake Michigan. Water Air Soil Pollut. 2: 497–514.

SCHELSKE, C. L. 1975. Silica and nitrate depletion as related to rate of eutrophication in Lakes Michigan, Huron, and Superior, p. 277–298. *In* A. D. Hasler [ed.] Coupling of land and water systems. Springer-Verlag New York Inc. New York, NY.

1985. Biogeochemical silica mass balances in Lake Michigan and Lake Superior. Biogeochemistry 1: 197–218.

SCHELSKE, C. L., C. O. DAVIS, AND L. E. FELDT. 1984a. Growth responses of river and lake phytoplankton populations in Lake Michigan water. Verh. Int. Ver. Limnol. 22: 445–451.

SCHELSKE, C. L., B. J. EADIE, AND G. L. KRAUSSE. 1984b. Measured and predicted fluxes of biogenic silica in Lake Michigan. Limnol. Oceanogr. 29: 99–110.

SCHELSKE, C. L., L. E. FELDT, M. A. SANTIAGO, AND E. F. STOERMER. 1972. Nutrient enrichment and its effect on phytoplankton production and species composition in Lake Superior, p. 149–165. *In* Proc. 15th Conf. Great Lakes Res. International Association for Great Lakes Research.

SCHELSKE, C. L., E. D. ROTHMAN, E. F. STOERMER, AND M. A. SANTIAGO. 1974. Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. Limnol. Oceanogr. 19: 409–419.

SCHELSKE, C. L., M. S. SIMMONS, AND L. E. FELDT. 1975. Phytoplankton responses to phosphorus and silica enrichments in Lake Michigan. Verh. Int. Ver. Limnol. 19: 911–921.

SCHELSKE, C. L., AND E. F. STOERMER. 1971. Eutrophication, silica depletion, and predicted changes in algal quality in Lake Michigan. Science (Wash., DC) 173: 423–424.

1972. Phosphorus, silica, and eutrophication of Lake Michigan, p. 157–171. *In* G. E. Likens [ed.] Nutrients and eutrophication, Special Symposia Vol. 1, American Society of Limnology and Oceanography. Allen Press, Lawrence, KS.

SCHELSKE, C. L., E. F. STOERMER, D. J. CONLEY, J. A. ROBBINS, AND R. M. GLOVER. 1983. Early eutrophication in the lower Great Lakes: new evidence from biogenic silica in sediments. Science (Wash., DC) 222: 320–322.

STOERMER, E. F., B. G. LADEWSKI, AND C. L. SCHELSKE. 1978. Population responses of Lake Michigan phytoplankton to nitrogen and phosphorus. Hydrobiologia 57: 249–265.

STOERMER, E. F., J. A. WOLIN, C. L. SCHELSKE, AND D. J. CONLEY. 1985. An assessment of ecological changes during the recent history of Lake Ontario based on siliceous algal microfossils preserved in the sediments. J. Phycol. 21: 257–276.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372.

Synopsis: Phosphorus–Plankton Dynamics Symposium[1]

Stephen J. Tarapchak

Great Lakes Environmental Research Laboratory, 2300 Washtenaw Avenue, Ann Arbor, MI 48104, USA

and Czesia Nalewajko

Life Sciences Division, Scarborough Campus, University of Toronto, Military Trail, West Hill, Ont. M1C 1A4

The concept of nutrient limitation is a cornerstone of phytoplankton production and seasonal succession theory (Tarapchak and Nalewajko 1986). Several crucial questions were debated during the symposium. First, *is the commonly accepted assumption of uniform orthophosphate (P_i) distribution in bulk solution correct*? For example, natural phytoplankton subjected to steady-state P_i supply rates and those pulsed with P_i exhibit major differences in species composition (e.g. Sommer 1985). If algae experience non-uniform P_i supplies, then the long-standing assumption that species competition occurs under steady-state P_i conditions in nature is totally inadequate. Clever experiments must be designed to determine to what extent phytoplankton dynamics are affected by "pulsed" P_i supplies, especially since actively feeding zooplankton are known to produce plumes with P_i concentrations several orders of magnitude higher than ambient bulk levels. Second, *two juxtaposed concepts in phytoplankton competition theory were debated: cell size versus interspecific differences in nutrient uptake capacity*. For example, Smith and Kalff (1985) argued that there is no partitioning of the gradient of P availability, and that competition occurs to the advantage of smaller cells. Conversely, Sommer and Kilham (1985) contended that the outcome of competition is determined by interspecific differences in the ability of species to take up and utilize P_i. This fundamental problem must be resolved if a unified theory of phytoplankton competition is to be developed. Third, *is our current concept of P-limited phytoplankton growth, developed primarily from laboratory monoculture studies, adequate to explain the relationships between P supply and phytoplankton growth in natural systems*? For example, Smith and Kalff (1981) demonstrated that, although Lake Memphremagog, Quebec, is considered highly P-limited, data suggest strongly that phytoplankton grow at relatively high rates, but do not synthesize the large quantities of alkaline phosphatase characteristic of P-limited algae. Algae apparently are able to obtain adequate P_i supplies despite the presence of only minute bulk ambient P_i concentrations, suggesting that these organisms either have exceptionally high-affinity P_i uptake systems, or they obtain P_i from sources other than the bulk ambient P_i pool. The anomaly might be explained by the fact that algae have adapated to chronically low bulk P_i concentrations in nature by synthesizing exceptionally high-affinity transport systems (Tarapchak and Herche 1986); however, the presence of high-affinity systems does not preclude the fact that algae may rely on other P sources.

The resolution of these three problems is crucial in order to advance our basic understanding of plankton dynamics and to develop improved nutrient bioassay techniques. The importance of nutrient limitation in shaping phytoplankton community structure has been addressed by Kilham (1986). Her data support the theory of competitive nutrient partitioning by showing that species assort themselves along resource gradients of P and Si in Lake Michigan. Further evidence for nutrient partitioning as opposed to the cell-size theory is imbedded in the bioassay experiments of Sakshaug and Olsen (1986). They show that phytoplankton in fresh and brackish Norwegian waters are P limited and that high-salinity waters are nutrient balanced or N limited. Their experiments in chemostats also demonstrate that the outcome of competition can be reversed when nutrient supplies are pulsed. Conversely, nutrient limitation in estuaries is highly variable, oscillating between degrees of N and P insufficiency. Experiments by D'Elia et al. (1986) also suggest that phytoplankton species in the Patuxent River estuary partition limiting N and P supplies and also that mixed communities can be limited by multiple nutrients.

Phosphorus Cycling

Research during the last 10 yr has demonstrated that the aquatic P cycle is far more complex than envisioned in the early 1970's (Tarapchak and Nalewajko 1986). For example, the conceptual model of Scavia (1980) separates particulate P into several inorganic and organic P fractions, defines several distinct dissolved P fractions, splits phytoplankton and bacteria into separate components, and includes compartments for fish and protozoa (Fig. 1). A principal impediment in developing a better understanding of how P controls primary and secondary production is the general lack of a quantitative perspective on whole-lake P cycling. For example, what are the major pathways for P_i uptake, how much of the epilimnetic P, relative to external supplies, is lost to the open-water sediments or littoral zone, and what are the primary P_i regenerative mechanisms in the epilimnion? The study by Levine et al. (1986) on whole-lake P cycling in Lake 227, northwestern Ontario, exemplifies the importance of such studies. Their work, for example, provides quantitative insights into rates of biological P utilization, exchange processes between dissolved and particulate P compartments, and losses of epilimnetic P to the hypolimnion, sediments, and littoral vegetation. Papers published in this

[1]GLERL Contribution No. 476.

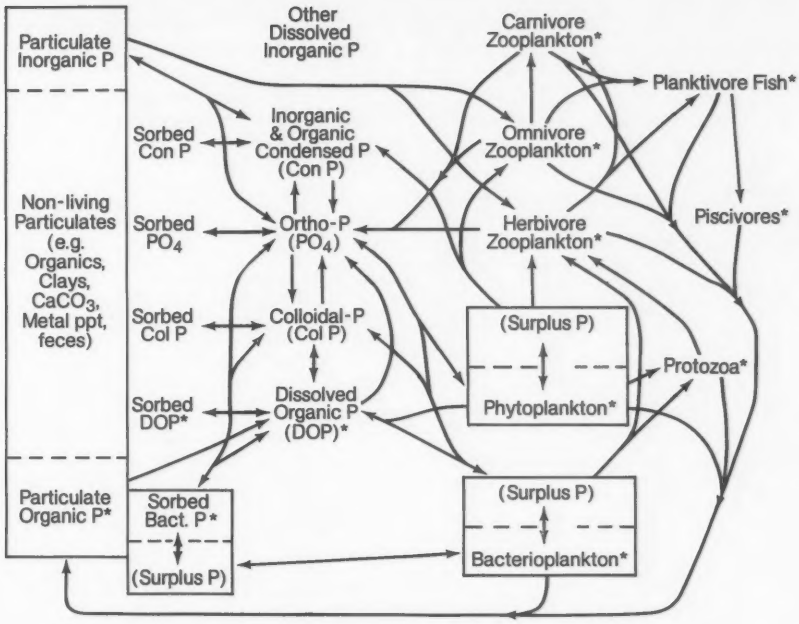


FIG. 1. Conceptual diagram of the phosphorus cycle in lakes (from Scavia 1980).

issue and recently by other scientists focus sharply on several critical research questions raised in the introduction (Tarapchak and Nalewajko 1986).

Orthophosphate Uptake

Phytoplankton growth in natural waters drives epilimnetic P cycling. The relationship between the P_i and phytoplankton compartments in natural systems cannot be modeled mechanistically because the rates of net P_i uptake by phytoplankton and de novo biomass synthesis cannot be quantified. This problem exists primarily because P_i pool size still cannot be accurately measured, and conventional tracers measure gross instead of net P_i uptake. The problem is further compounded by two factors. First, the variable light regimes experienced by algae in the water column may affect P_i uptake (Harris and Piccinin 1983; Nalewajko et al. 1986). Second, P_i uptake rates may not be dependent solely on external P_i and intracellular P concentrations. The presence of dissolved regulatory molecules may also affect P_i uptake in natural assemblages (Francko and Wetzel 1982; Karl and Craven 1980). Imaginative approaches are urgently required to devise methods for measuring P_i pool size, net microbial P_i uptake rates, and P uptake-coupled biomass synthesis rates in nature. Until these problems are resolved, the approach used by Auer et al. (1986) to quantify relationships between P availability and algal growth provides a suitable alternative. They have successfully applied the Monod and Droop models to field measurements of P and gross photosynthesis. The approach establishes an important conceptual foundation for relating P availability and phytoplankton growth in lakes of dissimilar trophic state.

Bacteria–Phytoplankton Competition

Modeling the P cycle requires the separation of algae and bacteria into functional components. Strong evidence that bacteria may outcompete algae for P_i has been presented by Currie et al. (1986). However, further studies are required to verify these results because other reports show that algae may outcompete bacteria for P_i (e.g. Berman 1985). Competition between algae and bacteria for P_i has important implications beyond the control of phytoplankton seasonal succession patterns. For example, if bacteria are using P_i as the principal P source, then the recycle mechanism for dissolved organic compounds (DOP) looms as a major, unanswered question. Are algae capable of utilizing DOP directly, or do they obtain P_i after enzymic degradation of DOP at the cell surface? Experiments by Heath (1986) on the availability of organic P compounds to plankton are instructive. His data show that P_i release from the DOP pool accounts for less than 1% of seston P_i uptake. These results suggest that DOP may not serve as a significant P source for microbial communities. If this is true, then how is DOP recycled? Could DOP be hydrolyzed by passage through the acidic guts of zooplankton? The nutrient or nutrients that limit algal and bacterial growth and the primary P sources of these organisms (both potential and realized) over a range of lake trophic conditions must be identified and the uptake rates quantified. Otherwise, P cycling in the lower food web cannot be understood or successfully modeled.

Phosphorus Regenerative Mechanisms

The relatively high phytoplankton growth rates in large P-limited lakes receiving minimal external P loadings begs the question: What are the relative P_i regenerative contributions of zooplankton, bacteria, enzymatic activity, and physical–chemical processes to the phytoplankton total P budget? P_i regeneration rates by zooplankton are directly proportional to water temperature, algal density, and predator hunger state, indicating that P_i regeneration will be spatially and seasonally variable (Bowers 1986). Experiments on microbial remineral-

ization of phytoplankton P show that microbial decomposers alone can supply P_i above the minimum cell quota for algal growth (De Pinto et al. 1986). Similarly, P_i recycling from the DOP pool by alkaline phosphatase activity and by photodependent release from UV-sensitive complexes are important regenerative mechanisms in Oklahoma lakes (Francko 1986). Collectively, these studies suggest that multiple regenerative mechanisms do operate in P-limited lakes as suggested by Wetzel (1983). However, the relative contributions of these mechanisms must be quantified with respect to phytoplankton demand in the water column of trophically variable lakes so that P controls on phytoplankton production can be understood.

Perspectives

Our understanding of the critical elements of aquatic P cycling that underlie phytoplankton–bacteria–zooplankton dynamics is far from complete. Two frequently ignored problems must be addressed if our understanding of plankton dynamics is to improve. First, the impact of "control from above" on phytoplankton productivity and species succession must be considered. Recent studies suggest that variations in lake productivity may, in fact, result from predation and herbivory rather than from nutrient supply. Carpenter et al. (1985) recently hypothesized that changes in abundance of piscivorous fishes have effects that cascade through food webs, producing systematic shifts in the biomass and productivity of zooplanktivores, herbivorous zooplankton, and phytoplankton. Second, efforts to understand nutrient-based phytoplankton competition must also consider the potential effects of heavy metals and synthetic toxic organic compounds on microbial physiology in the Great lakes system and elsewhere. For example, recent reports have clearly shown that concentrations of these substances in the Great Lakes are sufficiently high to significantly affect microbial growth (e.g. Lederman and Rhee 1982; IJC 1985).

Significant improvements in most open-water regions of the Great Lakes are expected from point-source P reduction programs implemented over the past decade (Vollenweider et al. 1980). The most visible result should be a decrease in plankton biomass and a shift in phytoplankton and zooplankton species composition toward more oligotrophic conditions, particularly in the lower Great Lakes as evidenced from the historical record of algae in sediments (Stoermer et al. 1985). A framework for future scientific research into P–plankton dynamics in the Great Lakes already exists. For example, the P–Si eutrophication hypothesis of Schelske and Stoermer, originally devised to explain the biological consequences of excessive P loadings, has now been extended to include the biogeochemistry of Si cycling in the Great lakes (Schelske et al. 1986). Kilham (1986) has demonstrated the role of limiting P and Si concentrations and the importance of P to Si ratios as controlling factors in phytoplankton seasonal succession. Moreover, shifts in fish population abundances may have dramatic effects on phytoplankton species composition and productivity. For example, burgeoning populations of stocked salmonids in Lake Michigan have reduced the alewife (*Alosa pseudoharengus*) population, allowing *Daphnia* to flourish (Scavia et al. 1986). Seston concentrations apparently have decreased, since *Daphnia* are more voracious and nonselective grazers than the previously dominant calanoid capepods.

The Great Lakes provide a truly unique setting for scientific investigation into P controls on production dynamics and P cycling as the system approaches new steady-state conditions (Lesht 1985). This symposium has been an extremely valuable vehicle for assembling and discussing current issues in P cycling. The ultimate success of any symposium can only be judged by how the published proceedings stimulate scientists to confront critical research questions. We hope this symposium serves that purpose.

References

AUER, M. T., M. S. KIESER, AND R. P. CANALE. 1986. Identification of critical nutrient levels through field verification of models for phosphorus and phytoplankton growth. Can. J. Fish. Aquat. Sci. 43: 379–388.

BERMAN, T. 1985. Uptake of [^{32}P] orthophosphate by algae and bacteria in Lake Kinneret. J. Plankton Res. 7: 71–84.

BOWERS, J. A. 1986. Phosphorus regeneration by the predatory copepod *Diacyclops thomasi*. Can. J. Fish. Aquat. Sci. 43: 361–365.

CARPENTER, S. R., J. R. HODGRUN, AND J. F. KITCHELL. 1985. Cascading trophic interactions and Lake Ecosystem productivity. BioScience. 35: 634–639.

CURRIE, D. J., E. BENTZEN, AND J. KALFF. 1986. Does algal–bacterial phosphorus partitioning vary among lakes? A comparative study of orthophosphate uptake and alkaline phosphatase activity in freshwater. Can. J. Fish. Aquat. Sci. 43: 311–318.

DE PINTO, J. V., T. C. YOUNG, J. S. BONNER, AND P. W. RODGERS. 1986. Microbial recycling of phytoplankton phosphorus. Can. J. Fish. Aquat. Sci. 43: 336–342.

D'ELIA, C. F., J. G. SANDERS, AND W. R. BOYNTON. 1986. Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures. Can. J. Fish. Aquat. Sci. 43: 397–406.

FRANCKO, D. A. 1986. Epilimnetic phosphorus cycling: influence of humic materials and iron on coexisting major mechanisms. Can. J. Fish. Aquat. Sci. 43: 302–310.

FRANCKO, D. A., AND R. G. WETZEL. 1982. The isolation of cyclic adenosine 3′:5′-monophosphate (cAMP) from lakes of differing trophic status: correlation with planktonic metabolic variables. Limnol. Oceanogr. 27: 27–38.

HARRIS, G. P., AND B. B. PICCININ. 1983. Phosphorus limitation and carbon metabolism in a unicellular alga: interaction between growth rate and the measurement of net and grass photosynthesis. J. Phycol. 19: 185–192.

HEATH, R. T. 1986. Dissolved organic phosphorus compounds: do they satisfy planktonic phosphate demand in summer? Can. J. Fish. Aquat. Sci. 43: 343–350.

INTERNATIONAL JOINT COMMISSION (IJC). 1985. Report on Great Lakes Water Quality. Great Lakes Water Quality Board, report to the International Joint Commission, presented Kingston, Ont. 212 p.

KARL, D. M., AND D. B. CRAVEN. 1980. Effects of alkaline phosphatase activity on nucleotide measurements in aquatic microbial communities. Appl. Environ. Microbiol. 40: 549–561.

KILHAM, S. S. 1986. Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient. Can. J. Fish. Aquat. Sci. 43: 351–360.

LEDERMAN, T. C., AND G-Y. RHEE. 1982. Influence of hexachlorobiphyl in Great Lakes phytoplankton in continuous culture. Can. J. Fish. Aquat. Sci. 29: 388–394.

LESHT, B. M. 1985. Time-dependent solution of multi-segment mass balance models of contaminants in the Great lakes. J. Great Lakes Res. 11: 182–189.

LEVINE, S. N., M. P. STAINTON, AND D. W. SCHINDLER. 1986. A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227, northwestern Ontario. Can. J. Fish. Aquat. Sci. 43: 366–378.

NALEWAJKO, C., B. PAUL, K. LEE, AND H. SHEAR. 1986. Light history, phosphorus status, and the occurrence of light stimulation or inhibition of phosphate uptake in Lake Superior phytoplankton and bacteria. Can. J. Fish. Aquat. Sci. 43: 329–335.

SAKSHAUG, E., AND Y. OLSEN. 1986. Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition. Can. J. Fish. Aquat. Sci. 43: 389–396.

SCAVIA, D. 1980. Conceptual model of phosphorus cycling, p. 119–140. *In* D. Scavia and R. Moll [ed.] Nutrient cycling in the Great Lakes: a summarization of factors regulating the cycling of phosphorus. Spec. Rep. No. 83, Great Lakes research Division, University of Michigan, Ann Arbor, MI.

SCAVIA, D., G. L. FAHNENSTIEL, M. S. EVANS, D. J. JUDE, AND J. T. LEHMAN.

1986. Influence of salmonid predation and weather on long-term water quality trends in Lake Michigan. Can. J. Fish. Aquat. Sci. 43: 435–443.

SCHELSKE, C. L., E. F. STOERMER, G. L. FAHNENSTIEL, AND M. HAIBACH. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. 43: 407–415.

SMITH, R. E. H., AND J. KALFF. 1981. The effect of phosphorus limitation on algal growth rates: evidence from alkaline phosphatase. Can. J. Fish. Aquat. Sci. 38: 1421–1427.

1985. Phosphorus competition among phytoplankton: a reply. Limnol. Oceanogr. 30: 440–444.

SOMMER, U. 1985. Comparisons between steady state and non-steady state competition: experiments with natural phytoplankton. Limnol. Oceanogr. 30: 335–346.

SOMMER, U., AND S. S. KILHAM. 1985. Phytoplankton natural community competition experiments: a reinterpretation. Limnol. Oceanogr. 30: 436–440.

STOERMER, E. F., J. A. WOLIN, C. L. SCHELSKE, AND D. J. CONLEY. 1985. Postsettlement diatom succession in the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 42: 754–767.

TARAPCHAK, S. J., AND L. R. HERCHE. 1986. Phosphate uptake by microorganisms in lake water: deviations from simple Michaelis–Menten kinetics. Can. J. Fish. Aquat. Sci. 43: 319–328.

TARAPCHAK, S. J., AND C. NALEWAJKO. 1986. Introduction: Phosphorus–Plankton Dynamics Symposium. Can. J. Fish. Aquat. Sci. 43: 293–301.

VOLLENWEIDER, R. A., W. RAST, AND J. KEREKES. 1980. The phosphorus loading concept and Great Lakes eutrophication, p. 207–234. *In* R. C. Loer, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Publishers, Inc., Ann Arbor, MI.

WETZEL, R. G. 1983. Limnology. 2nd ed. Saunders College Publishing.

Zooplankton Species Abundance and Biomass in Relation to Occurrence of *Mysis relicta* (Malacostraca: Mysidacea)

Redwood W. Nero and W. Gary Sprules

Department of Zoology, Erindale Campus, University of Toronto, Mississauga, Ont. L5L 1C6

Nero, R. W., and W. G. Sprules. 1986. Zooplankton species abundance and biomass in relation to occurrence of *Mysis relicta* (Malacostraca: Mysidacea). Can. J. Fish. Aquat. Sci. 43: 420–434.

Year-long comparisons of the occurrence and abundance of zooplankton between two lakes where *Mysis relicta* is endemic and two where it is not show that in the former, hypolimnetic species *Daphnia longiremis, Eubosmina longispina, Cyclops scutifer,* and *Diaptomus sanguineus* are rare. Five other cladocerans were also lower in abundance in hypolimnetic strata and during isothermal conditions. *Diaphanosoma* spp. were more abundant in the metalimnion of lakes with *Mysis*; we suggest a competitive release through *Mysis* predation on *Daphnia*. Because each pair of lakes is comparable with respect to morphometry and chemistry, nonpredatory influences do not account for the observed distribution of zooplankton. Such species differences are also identical to trends occurring in a canonical analysis of zooplankton abundance for 497 lakes in eastern Ontario and western Quebec and corroborate declines in Cladocera associated with introductions of *M. relicta* into lakes and reservoirs.

Des comparaisons sur une base annuelle quant à la présence et à l'abondance de zooplancton entre deux lacs où *Mysis relicta* est endémique et deux autres où elle ne l'est pas, indiquent que dans le premier cas les espèces de l'hypolimnion, *Daphnia longiremis, Eubosmina longispina, Cyclops scutifer* et *Diaptomus sanguineus*, sont rares. Cinq autres cladocères étaient également moins abondants dans les strates de l'hypolimnion et dans des conditions d'isothermie. *Diaphanosoma* spp. était plus abondante dans le métalimnion de lacs où l'on retrouve *Mysis*; on suggère un avantage dû à la compétition résultant de l'action prédatrice de *Mysis* sur *Daphnia*; puisque les deux paires de lacs sont comparables quant à leur morphométrie et à leur chimie, les influences autres que la prédation n'expliquent pas la distribution observée du zooplancton. De telles différences au niveau des espèces sont également identiques aux tendances manifestées par une analyse canonique de l'abondance du zooplancton dans 497 lacs de l'est de l'Ontario et de l'ouest du Québec, et confirment le déclin chez la population de *Cladocera* associé à l'introduction de *M. relicta* dans les lacs et les réservoirs.

Received May 31, 1985
Accepted October 11, 1985
(J8274)

Reçu le 31 mai 1985
Accepté le 11 octobre 1985

Mysis relicta has been introduced into many lakes and reservoirs in the northeastern United States, the interior of British Columbia, and Scandinavian lakes and reservoirs to increase fish production by providing a new forage item for intermediate-sized salmonids (Furst 1981; Gosho 1975). However, some studies have shown that *Mysis*[1] predation on cladoceran zooplankton alters the trophic structure of lakes to the detriment of target fish species (Morgan et al. 1978; Rieman and Falter 1981). To better understand effects of *Mysis* predation on Cladocera and other susceptible species, mysid–zooplankton interactions have been studied in lakes where *Mysis* have been introduced (Lasenby and Furst 1981; Rieman and Falter 1981; Threlkeld 1981; and others). Most of these studies, and work on other mysid species (Murtaugh 1983), show that mysids can be voracious predators that consume slower moving zooplankton (Ramcharan et al. 1985). Based on these findings we would expect *Mysis* to have a major influence on zooplankton in lakes where they occur naturally. Although the predation ecology of endemic *Mysis* populations (Lasenby and Langford 1973; Grossnickle 1978; Bowers and Vanderploeg 1982) has been examined in a few studies, none has determined the extent to which *Mysis* influence zooplankton in these lakes.

[1]For simplicity, some species are henceforth referred to by genus only.

In eastern North America, *Mysis* occurs naturally in lakes which were once part of a glacial lake (Segerstrale 1962; Dadswell 1974). In a survey of 696 lakes distributed across eastern North America, Dadswell (1974) and Carter et al. (1980) identified *Mysis, Senecella calanoides, Limnocalanus macrurus*, and *Diaptomus sicilis* as "glacial opportunists" that acquired their present distribution through postglacial water systems. For the purposes of this study, the abundance of all other zooplankton species is assumed to be limited by current habitat suitability and not by previous dispersal events (Carter et al. 1980). Through a multivariate analysis of the zooplankton fauna of these lakes, Roff et al. (1981) found that the lakes form two distinct groups that reflect their glacial history. In this study we test the hypothesis that predation on zooplankton by *Mysis* is the major determinant of this pattern by first more explicitly examining data of Roff et al. (1981) with respect to the occurrence of *Mysis* and second, dealing with prey distributions in native lakes for *Mysis* in a detail not hitherto attempted.

Materials and Methods

Zooplankton Abundance Data of Roff et al. (1981)

In their original principal components analysis, Roff et al. (1981) did not exclude the glacial opportunists from their ordi-

TABLE 1. Physical characteristics of lakes selected for a comparison of zooplankton composition and biomass in central Ontario (Ontario Ministry of Natural Resources, Minden, Ont., unpubl. data).

Lake	Lake code	Latitude	Longitude	Relict	Area (ha)	Volume (million m^3)	Max. depth (m)	Mean depth (m)
Gull	MY1	44°51′	78°47′	Yes	996	163.8	49.1	16.5
Kashagawigamog	NR1	44°59′	78°36′	No	528	83.2	40.1	15.8
Bob	MY2	44°55′	78°47′	Yes	220	39.9	64.0	18.1
Soyers	NR2	45°02′	78°37′	No	329	63.5	49.1	19.0
Boshkung	MY3	45°04′	78°44′	Yes	716	165.9	71.0	23.2
Halls	NR3	45°06′	78°45′	No	540	152.8	69.5	28.3
Fortesque[a]	MY4	44°50′	78°26′	Yes	79	9.3	28.7	11.8
Salmon[a]	NR4	44°59′	78°27′	No	172	19.5	30.5	11.3
Crystal	MY5	44°45′	78°30′	Yes	443	52.3	36.0	11.8
Koshlong	NR5	44°58′	78°29′	No	401	41.6	42.7	10.4

[a]Paloheimo and Zimmerman (1983).

nation. As a result, good separation of lakes with differing glacial histories was primairly along their first two principal components which correlated well with abundances of the glacial opportunists. Although their original analysis provides a suitable description of overall structure of the data, it fails to elucidate differences between relict and nonrelict lakes which could be attributed to glacial opportunist predators. Hence we used canonical discriminant analysis of their coded abundance of 23 zooplankters, all species that are distributed independently of glaciation, to find which species best separate three lake types: relict lakes with *Mysis* ($n = 178$); relict lakes without *Mysis* ($n = 76$) (during dispersal events, a number of glacial lakes did not receive *Mysis* (Dadswell 1974)); and nonrelict lakes (all without *Mysis* ($n = 243$)). The idea is that species emerging as good discriminators among lake types are those affected directly or indirectly by *Mysis* predation. Analysis was restricted to 497 lakes with basin areas less than 10 000 km^2 and surface areas less than 10 000 ha in order to eliminate large and diverse lakes where the influence of *Mysis* may be confounded by large-scale patchiness. Discrimination was done on the standardized species data using canonical discriminant analysis (Ray 1982).

Description of Study Lakes

Results of the foregoing analysis are compared with differences in the zooplankton fauna among 10 central Ontario lakes, 5 that contain *Mysis* (relict lakes) and five that do not (nonrelict lakes). Because lake area and depth are primary determinants of community type in oligotrophic lakes (Patalas 1971), we paired lakes having similar morphometry to minimize morphometric influences on species distribution (Table 1). We designated "*Mysis*" lake number "1" as "MY1" and "nonrelict" lake number "1" as "NR1." We considered the first two pairs (MY1/NR1 and MY2/NR2) the most similar in lake shape, orientation, and morphometry and compared them based on a year-long study of their zooplankton. An additional three pairs of less similar lakes were used for a single spring zooplankton survey.

Historically, lakes MY1, NR1, MY2 and NR2 are identical, having been free of continental ice since ca. 12 000 B.P. (Prest 1970). Besides inundation and inoculation of MY1 and MY2 with glacial opportunist species ca. 11 800 B.P. (Prest 1970), no major events have occurred within the watersheds of these lakes. Because all four lakes lie on calcareous meta-sediments (National Research Council of Canada 1981), they are uninfluenced by acid precipitation which occurs throughout the region (Dillon et al. 1978). Water renewal times in Lakes MY1, NR1, MY2, and NR2 are sufficiently long (0.3, 0.7, 2.4, and 2.9 yr, respectively) that differences in zooplankton composition among lakes cannot be attributed to washout (Brook and Woodward 1956).

Background Data

We sampled at a deep central location in all lakes except MY1 where we collected samples from the north basin (maximum depth 45 m) due to its close proximity to a University of Toronto field station. Between 22 May 1982 and 9 August 1983, temperature–depth profiles were obtained for Lakes MY1, NR1, MY2, and NR2 using a Montedoro Whitney model TC-5A thermistor at the time of zooplankton sampling.

In lakes MY1, NR1, MY2, and NR2 we determined Secchi depths five to seven times during summer 1983 and collected epilimnetic water samples (0.3 m depth) four times during May to August 1983 for determinations of color, total Kjeldahl nitrogen (TN), total phosphorus (TP), and chlorophyll *a*. Analyses were performed by the Ontario Ministry of the Environment at their Dorset and Rexdale laboratories. We also collected water samples for oxygen determination (APHA 1975) from the maximum depth of each lake on 8 August 1983 using a 2-L Van Dorn bottle.

As a simple measure of fish density, echo surveys of pelagic fish in MY1 and NR1 were made in late September 1983 by J. R. M. Kelso (Department of Fisheries and Oceans, Sault Ste. Marie, Ont.) using acoustic techniques (Kelso et al. 1974; Kelso and Minns 1975). Such an analysis of echograms gives excellent correlations with midwater trawl catches (Kelso et al. 1974). Approximately 0.48 and 0.31% of the volumes of MY1 and NR1, respectively, were surveyed in this manner.

We obtained density estimates of *Mysis* populations from vertical tows of a 1-m^2 net (Nero 1982) and from samples intended for zooplankton enumeration. We took all 1-m^2 tows at least 1 h after sunset when most *Mysis* would be in the water column (Beeton 1960). In MY1 we collected three vertical tows at the north station during sampling trips conducted every 2–5 wk from May 1982 through to August 1983 except for the May, June, and December 1982 trips during which we took a single tow. To determine the extent of the vertical migration of *Mysis* in MY1, we collected *Mysis* with a series of progres-

sively deeper vertical tows (see Nero and Davies 1982) at midnight on 21 May 1982, 31 May 1983, and 3 August 1983. We preserved all *Mysis* in 70% ethanol upon collection. Adult and young-of-the-year *Mysis* were counted in entire samples, but during January to March these stages could not be distinguished. All counts were corrected for a measured net efficiency of 87% calculated from a current meter profile measured across the net mouth at a towing speed of 0.33 $m \cdot s^{-1}$.

All zooplankton samples were collected with a 46-cm-diameter net with a 2-m-long cone of 150-μm synthetic netting hauled from near-bottom to surface. We measured this net's filtering efficiency at 70% when towed at 0.33 $m \cdot s^{-1}$ (Yan et al. 1985). Although the large mesh size would not allow efficient capture of rotifers and small nauplii, the coarse mesh and large mouth area were chosen to efficiently capture large, fast-swimming calanoid copepods (de Bernardi 1984). We used a Hensen closing mechanism (de Bernardi 1984) to obtain vertical hauls within a specific depth stratum. During sampling through ice in the winter, a zooplankton net as described above was fitted with a square collapsible frame (Nero 1982).

For comparisons of species abundance between lake pairs MY1/NR1 and MY2/NR2, samples were collected approximately monthly on 17 dates in MY1 and NR1 between 21 May 1982 and 10 August 1983 and for MY2 and NR2 on 25 May and 22 October 1982 and approximately monthly on 7 dates between 27 January 1983 and 8 August 1983. We sampled MY1 and NR1 at night just prior to collections for *Mysis*, and for convenience, we sampled MY2 and NR2 in the daytime. Because the upward extent of *Mysis* migration is restricted by water temperatures over 14–18°C (Beeton 1960; Nero and Davies 1982), zooplankton were collected under two different conditions. "Isothermal" conditions are those cold enough for *Mysis* to migrate throughout the water column (defined here as less than 16°C). "Stratified" conditions are those with an epilimnion devoid of *Mysis* (temperature >18°C), a metalimnion, partially available to *Mysis* (8–18°C), and an 4–8°C hypolimnion divided at 20–25 m into an upper and lower hypolimnion. Three replicate samples were collected from each stratum on most dates. An additional survey was made of five lake pairs (MY1/NR1 to MY5/NR5) during isothermal conditions on 16 May 1983. Three whole-column vertical tows were collected from each lake.

All samples were preserved in 70% ethanol. Species were identified and a total of 300 animals enumerated from subsamples of between 0.5 and 16%. Entire samples were enumerated for *Mysis* and rare species. Animals were examined with a compound microscope and identified using the taxonomic keys of Smith and Fernando (1978) for copepods and Deevey and Deevey (1971) and Brandlova et al. (1972) for Cladocera. All animals were identified to species except for the genus *Diaphanosoma*. Small copepods were grouped as either nauplii, calanoid copepodites 1–3, or cyclopoid copepodites 1–2. Rotifers were not counted.

We made estimates of zooplankton biomass from pooled samples created by combining aliquots from replicate samples. At least 240 animals from each sample were measured and classified into 13 taxonomic categories using a microcomputer-based measuring system (Sprules et al. 1981). Biomass for each category was calculated by summing the wet weight of each individual (calculated from length–weight relationships selected from the literature (W. G. Sprules, University of Toronto, unpubl. data)) and correcting for subsample volume and net efficiency.

Where data were sufficiently numerous, species abundances were compared between lake pairs using a Wilcoxon signed ranks test (Conover 1971). Otherwise, simple trends in abundances of species in lake pairs were noted. To display trends through time in species associations in the lake pairs, we used an ordination technique. Numerical abundances of 20 species in 96 samples were made more linear using the natural log $(1 + X)$ transformation. Ordination of samples on the basis of species data was done by detrended correspondence analysis (DCA) (Gauch 1982), an ordination technique allowing a community-centered description of heterogeneous species abundance data, which is more appropriate for nonlinear species abundance gradients than most other ordination techniques (Gauch 1982). For the survey of five lake pairs during isothermal conditions, comparisons of species abundance within lake pairs were made using a two-sample *t*-test.

Results

Zooplankton Abundance Data of Roff et al. (1981)

In our canonical discriminant analysis of the species abundance data of Roff et al. (1981), the first canonical variate, which separates lakes with and without *Mysis* (negative and positive ends of variate, respectively), accounts for 41% of overall variance in the species abundance data. The second canonical variate, separating relict lakes without *Mysis* from nonrelict lakes, accounts for only 8% of the variance. Thus, associations of nonrelict zooplankton species more strongly reflect presence or absence of *Mysis* than they do glacial history. Three species characteristic of hypolimnia, *Eubosmina longispina*, *Daphnia longiremis*, and *Cyclops scutifer* (vertical preference of species based on Carter et al. (1980) and R. W. Nero, unpubl. data) show strong positive correlations with the first canonical variate and are therefore characteristic of non-*Mysis* lakes (Table 2). The next six weaker positive correlations are species of *Daphnia*, *Holopedium gibberum*, *Sida crystallina*, and *Chaoborus punctipennis*. At the other extreme is *Diaphanosoma* having a strong negative correlation with the first canonical variate and thus characteristic of *Mysis* lakes. The next 10 species exhibit weak negative correlations and are typically considered epilimnetic species (Table 2). Overall, in this large set of lakes ($n = 497$), distributed over a wide geographic area, hypolimnetic Cladocera (and one cyclopoid) are less abundant in *Mysis* lakes than in non-*Mysis* lakes. The reverse is true for some epilimnetic species.

Background Data

Thermal regimes of Lakes MY1, NR1, MY2, and NR2 are almost identical with mean thermocline depths of 8.4, 7.2, 6.0, and 6.4 m, respectively, and maximum epilimnetic temperatures of 25.1, 25.5, 25.1, and 25.2°C, respectively. These lakes are all well oxygenated with minimum lower hypolimnetic oxygen concentrations of 2 $mg \cdot L^{-1}$.

Values of alkalinity, conductivity, and total dissolved solids, calcium, chlorophyll *a*, and TN suggest that Lakes NR1 and NR2 are richer than Lakes MY1 and MY2 (1.2–1.5 times greater, Table 3). However, TP, the major limiting nutrient in Precambrian shield lakes (Schindler 1977), is almost identical in all four lakes (9.0, 9.0, 8.6, and 9.0 $\mu g \cdot L^{-1}$ in MY1, NR1, MY2, and NR2, respectively) and are comparable with TP values in other oligotrophic lakes in south-central Ontario (Paloheimo and Zimmerman 1983). In addition, plots of chlo-

TABLE 2. Correlations of zooplankton abundances in 497 lakes with first and second canonical variates from canonical discriminant analysis. Asterisks indicate significant correlations, $P \leq 0.05$, 495 df.

Species	Canonical variate I	Canonical variate II
Eubosmina longispina	0.59*	0.05
Cyclops scutifer	0.55*	−0.45*
Daphnia longiremis	0.55*	0.35*
Daphnia pulex	0.35*	0.33*
Daphnia catawba	0.23*	−0.16*
Daphnia dubia	0.16*	−0.03
Holopedium gibberum	0.14*	−0.01
Sida crystalina	0.13*	−0.13*
Chaoborus punctipennis	0.09*	−0.11*
Eubosmina tubicen	0.03	−0.19*
Mesocyclops edax	−0.04	−0.04
Diaptomus minutus	−0.05	−0.37*
Daphnia galeata mendotae	−0.09*	0.01
Cyclops vernalis	−0.09*	0.03
Diaptomus oregonensis	−0.11*	0.08
Leptodora kindtii	−0.11*	−0.04
Epischura lacustris	−0.12*	0.04
Ceriodaphnia lacustris	−0.15*	0.30*
Diacyclops thomasi	−0.17*	0.47*
Polyphemus pediculus	−0.17*	−0.11*
Daphnia retrocurva	−0.22*	0.33*
Bosmina longirostris	−0.29*	0.10*
Diaphanosoma spp.	−0.40*	0.03

rophyll *a* against TP for each lake on all sampling dates are indicative of biological response to nutrient availability (Straskraba 1980), and show no apparent differences in productivity between lakes.

Data on fish species in lakes MY1, NR1, MY2, and NR2 are from gill net surveys carried out by the Ontario Ministry of Natural Resources, Minden, Ont. At least one member of the genera *Salvelinus* and *Coregonus* and the families Catostomidae, Percidae, and Centrarchidae occurred in each of the four main study lakes. Echo counts of fish from MY1 and NR1 indicate that fish populations are of similar densities. Volume-weighted averages across depth strata are 3.89 and 3.85 fish·10 000 m^{-3} for MY1 and NR1, respectively.

Glacial Opportunists

In MY1, *Mysis* is very abundant at the north station (Fig. 1) ranging from 200 Ind·m^{-2} in November 1982 to approximately 1000 Ind·m^{-2} in June 1983. Young-of-the-year were a major proportion of the population. Seasonal changes in age composition at this station may reflect seasonal changes in horizontal distribution of adult and young-of-the-year cohorts (Morgan and Threlkeld 1982). For MY2, estimates of *Mysis* densities at a single central station and from a lake-wide average estimate are about half that for MY1 during the same period (Fig. 1). On all dates sampled in MY1, *Mysis* migrated vertically into the water column at night, being restricted by epilimnetic temperatures of 17°C.

Counts of *Mysis*, *Limnocalanus*, and *Senecella* from samples obtained using the 46-cm-diameter net were used to determine seasonal average densities of these species in the water column of MY1 at night, for both isothermal and stratified conditions (Fig. 2). For both adult and young-of-the-year *Mysis* these

TABLE 3. Chemical characteristics of lakes MY1, MY2, NR1, and NR2.

Variable	MY1	NR1	MY2	NR2
Mean summer Secchi (m)	5.0	5.4	5.4	4.0
Color (Hazen units)	13	20	22	32
pH	7.05[a]	7.36[a]	7.05[a]	7.16[a]
Total inflection point alkalinity (μeq.·L^{-1})	317[b]	450[b]	180[b]	303[b]
Conductivity (μS·cm^{-1}, 25°C)	59[a]	80[a]	45[a]	61[a]
Total dissolved solids (mg·L^{-1})	55.3[c]	61.8[c]	23.3[d]	32.6[c]
Calcium (mg·L^{-1})	6.4[a]	9.0[a]	4.9[a]	6.3[a]
Chlorophyll *a* (μg·L^{-1})	2.0	3.0	1.4	2.0
Total Kjeldahl N (μg·L^{-1})	240	289	275	318
Total P (μg·L^{-1})	9.0	9.0	8.6	9.0
Aluminum (μg·L^{-1})	10[a]	4[a]	10[a]	17[a]
Zinc (μg·L^{-1})	6[a]	4[a]	6[a]	4[a]
Iron (μg·L^{-1})	75[a]	<15[a]	120[a]	60[a]
Manganese (μg·L^{-1})	8[a]	6[a]	8[a]	8[a]

[a]Yan et al. (1985).
[b]Ontario Ministry of the Environment (1981).
[c]Summer 1975 measurements, Ontario Ministry of Natural Resources, Minden, unpubl. data.
[d]Summer 1970 measurements, Ontario Ministry of Natural Resources, Minden, unpubl. data.

estimates were statistically similar to those made using the 1-m^2 net (Paired *t*-test, $n = 17$, $P > 0.4$), indicating good agreement between the two sampling methods. Summer abundance of *Mysis* is about twice that of the winter; for *Limnocalanus* and *Senecella* they are about five times more abundant in the summer. During stratification, densities of all three species ranged widely (Fig. 2), and they rarely occurred in the epilimnion. The highest *Mysis* densities occurred in the metalimnion at 4.3 adults·m^{-3} and 25 young-of-the-year·m^{-3}. *Senecella* was distributed evenly in the metalimnion and hypolimnion at 84−106 Ind·m^{-3}. *Limnocalanus* was more abundant in the lower hypolimnion than in either the metalimnion or upper hypolimnion (Fig. 2). Both *Limnocalanus* and *Senecella* were absent in MY2.

Prey Species

In MY1, prey species most susceptible to *Mysis* feeding are daphnids and bosminids, to a lesser extent *Epischura*, Cyclopoids, and *Holopedium*, and least *Diaptomus*, *Limnocalanus*, and *Senecella* (Nero and Sprules 1986). As some of these species were very rare during spring isothermal conditions, only those with abundances of 0.01 Ind·L^{-1} or greater were considered in the spring survey (Fig. 3). Nonrelict lakes have higher abundances of cladocerans (*Daphnia pulex*, *D. longiremis*, *Bosmina longirostris*, and *H. gibberum*). As neither

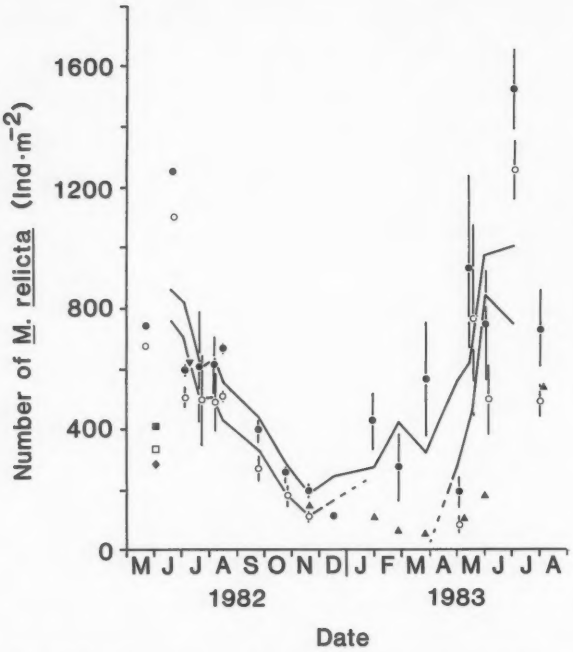


FIG. 1. Densities of *Mysis relicta* at night in MY1 at the north basin sampling station (●, total population; ○, young-of-the-year). Line is three-point running average; broken lines indicate recruitment of young-of-the-year into the adult population in January 1983 and birth of new young in April 1983. ▲, average density for the north basin; ▼, average density for the main lake. For MY2 central station areal densities: ■, total number; □, young-of-the-year; ♦, average lake-wide density. Vertical lines denote 95% confidence limits.

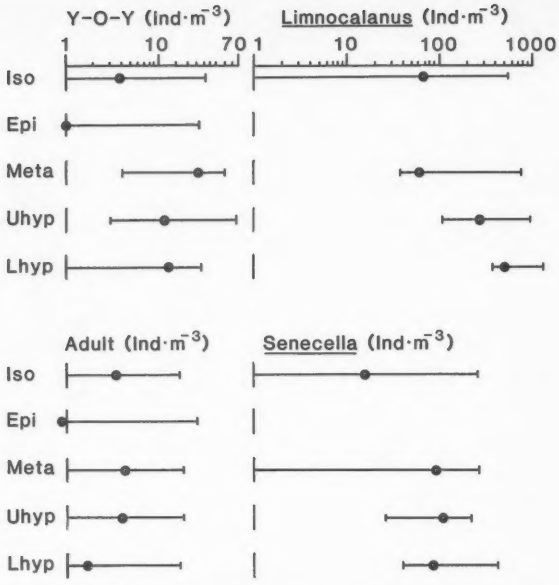


FIG. 2. Night-time seasonal median densities and ranges (horizontal bars) for *Mysis relicta*, *Limnocalanus macrurus*, and *Senecella calanoides* at the north basin of MY1 for summer 1982 to summer 1983. YOY, young-of-the-year *Mysis*; Adult, adult *Mysis*. Strata: Iso, isothermal; Epi, epilimnetic; Meta, metalimnetic; Uhyp, upper hypolimnion; Lhyp, lower hypolimnion.

Limnocalanus nor *Senecella* occur in MY2 and MY4, differences in cladoceran abundance are more likely due to predation by *Mysis* rather than predation by *Limnocalanus* and *Senecella*. Low cladoceran abundances in lakes with *Mysis* cannot be accounted for by cyclopoid predation because cyclopoid copepodites, *Cyclops*, and *Mesocyclops edax* are all more abundant in the nonrelict lakes (Fig. 3). In addition, low abundances of these cyclopoids and *Diaptomus sanguineus* in lakes with *Mysis* may be due to predation by *Mysis*. For four other species, calanoid copepodites, and nauplii there are no clear trends (Fig. 3).

Differences in zooplankton abundance between both lake pairs (MY1/NR1 and MY2/NR2) for all seasons are attributed to *Mysis* predation alone, and not predation from *Limnocalanus* and *Senecella* because these two species are absent in MY2. Some hypolimnetic species which were always very rare or absent in MY1 and MY2 are abundant in NR1 and NR2 during isothermal conditions and in hypolimnetic strata (category A, Table 4). This is evident from the seasonal abundance of *D. longiremis* (Fig. 4). *Daphnia dubia* and *Chydorus sphaericus* are two epilimnetic Cladocera which are lower in abundance in the epilimnion and metalimnion of both MY1 and MY2 than in NR1 and NR2 (category B). Seasonal abundance of *D. dubia* shows this well (Fig. 5). *Holopedium*, *Daphnia galeata mendotae*, and *Bosmina* are abundant in the epilimnion in all four lakes but have lower abundances in MY1 and MY2 in some part of the hypolimnion or during isothermal conditions (see Fig. 6 for *Bosmina*) (category C, Table 4). Differences for *Diacyclops thomasi* are unclear, as this species is lower in abundance in the hypolimnia, but not during isothermal conditions. This species has been placed with nine other "indifferent" species that show no clear differences in abundance between lakes (Table 4). An example of these species is the calanoid copepodites 1−3 which are present at all times in the four lakes (Fig. 7). Cyclopoid copepodites 1−2 and *Diaphanosoma* are more abundant in the metalimnion of MY1 and MY2 than in NR1 and NR2 (Table 4) (see Fig. 8 for *Diaphanosoma*).

The results of the detrended correspondence analysis (DCA) can be plotted to show relative location of samples in terms of the abundances of their composite species (Fig. 9). Samples close together have a more similar species composition and abundance than those further apart. Although all four lakes were ordinated together, each pair is plotted separately for clarity. Axes 1 and 2 have high eigenvalues (0.145 and 0.100, respectively), indicating high relative variance incorporated in these two axes. Axes 3 and 4 have lower values (0.041 and 0.027, respectively) and could not be meaningfully interpreted or plotted. Epilimnetic and metalimnetic samples group towards the upper left, and lower hypolimnion samples group towards the bottom right (Fig. 9). Samples from lakes without *Mysis* (NR1 and NR2) are located more towards the upper right than two lakes with *Mysis* (MY1 and MY2). Because more samples from MY1 and NR1 were included in this ordination (66) than from MY2 and NR2 (30), the ordination is more strongly influenced by differences between MY1 and NR1. Preliminary ordinations of MY2 and NR2 alone showed less

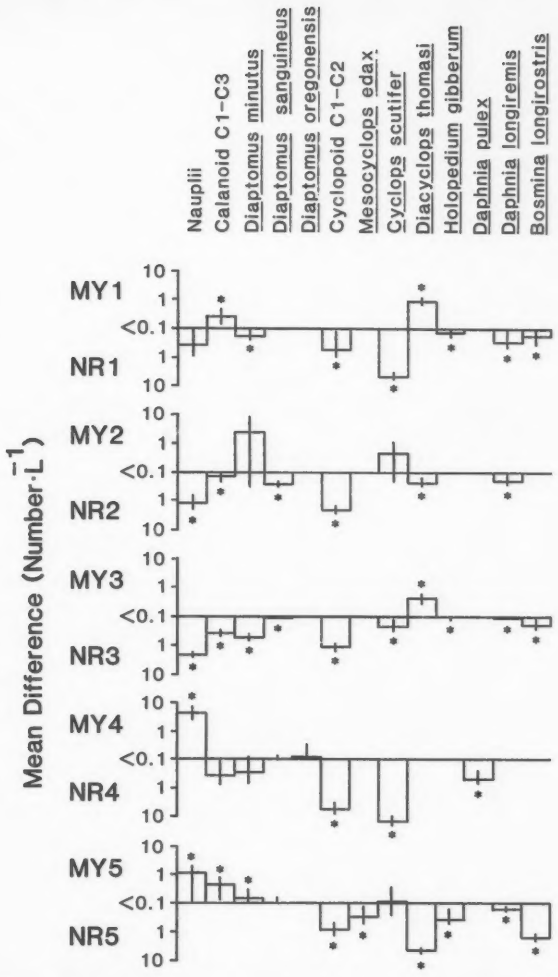


FIG. 3. Mean difference in abundance of zooplankton species and groups for isothermal conditions on 16 May 1983 in five pairs of lakes, where one contains *Mysis* (MY) and the other is a nonrelict lake without *Mysis* (NR). Column direction indicates which lake has a greater abundance. An asterisk indicates a significant difference at $P \leq 0.05$, two-sample *t*-test, 4 df. Vertical bars represent 95% confidence intervals about the mean difference.

separation along axis 2, likely because of the greater amount of variance in this smaller set of data.

Concurrent with the sample ordination is an ordination of species (Fig. 10). Each point represents the peak abundance or average occurrence of a particular species with respect to the sample ordination. DCA produces both ordinations simultaneously. Species more representative of epilimnetic directions (to the left on axis 1) are *D. dubia, Chydorus, Holopedium, Epischura*, and *Mesocyclops*. Four species characteristic of the NR1 and NR2 direction (upper right) are *D. sanguineus, D. longiremis, Eubosmina*, and *Cyclops*, all species which mainly occur in the hypolimnion of NR1 and NR2. *Cyclops* also characterizes the isothermal direction in NR1 and NR2. Species in the MY1 and MY2 direction are *Tropocyclops prasinus mexicanus* and possibly *Diaphanosoma* and *Diaptomus minutus*; *T. p. mexicanus* also characterizes isothermal conditions in the MY1 and MY2 direction.

TABLE 4. Differences in zooplankton abundance between two relict lakes with *Mysis* (MY1 and MY2) and two nonrelict lakes without *Mysis* (NR1 and NR2) (see text for statistical tests). −, lower abundance in *Mysis* lake; +, higher abundance in *Mysis* lake; ○, equal abundance; ·, insufficient data for statistical tests. Strata: E, epilimnion; M, metalimnion; U, upper hypolimnion; L, lower hypolimnion; I, isothermal. Species categories: A, hypolimnetic species scarce in MY1 and MY2 under all conditions; B, epilimnetic species rare in MY1 and MY2 under all conditions; C, species abundant in the epilimnion of MY1 and MY2 but absent in the deeper waters and during isothermal conditions; D, species showing no clear trends; E, species more abundant in MY1 and MY2.

Species	Category	Stratum E	M	U	L	I
Diaptomus sanguineus	A	·	−	−	−	−
Daphnia longiremis	A	−	−	−	−	−
Eubosmina longispina	A	·	−	−	−	−
Daphnia dubia	B	−	−	−	·	·
Chydorus sphaericus	B	−	−		·	−
Holopedium gibberum	C	○	−	·	·	−
Daphnia galeata mendotae	C	○	○	○	·	−
Bosmina longirostris	C	○	○	○	−	−
Calanoid copepodites 1−3[a]	D	○	○	○	○	○
Cyclops scutifer[b]	D	○	○	○	○	○
Diacyclops thomasi	D	○	○	−	−	○
Copepod nauplii	D	○	○	○	○	○
Epischura lacustris	D	○	○	·	·	·
Diaptomus minutus	D	○	○	○	○	○
D. oregonensis	D	○	○	○	·	○
Tropocyclops p. *mexicanus*	D	○	○	·	·	○
Mesocyclops edax	D	○	○	○	·	○
Cladoceran neonates	D	○	·	·	·	○
Cyclopoid copepodites 1−2	E	○	+	○	○	○
Diaphanosoma spp.[c]	E	○	+	○	○	○

[a]For the epilimnion, MY1 < NR1.
[b]For the upper hypolimnion and isothermal strata, MY1 < NR1.
[c]For the epilimnion, MY1 > NR1.

Although the lakes are similar in amount of total biomass during stratified and isothermal conditions, each species' contribution to this biomass varies greatly between lakes (Fig. 11). The greatest biomass occurs in the metalimnion of both lakes where large differences in species' group contribution occurs. Cladoceran biomass contributes only 9% in MY1, but 57% in NR1. In MY1 this difference is made up by *Mysis* which accounts for 47% and *Senecella* which accounts for 9%. In the upper and lower hypolimnion, total biomass in MY1 is about twice that of NR1. Cladocera contribute 20−33% in NR1, while in MY1, most biomass is contributed by four glacial relict species, *Mysis, Limnocalanus, Senecella*, and *Diaptomus sicilis*. Epilimnion biomass is somewhat similar in both lakes, with Cladocera accounting for 50−75% and *Diaptomus* spp. and cyclopoids most of the remaining 25−50%.

During isothermal conditions, total zooplankton biomass is similar in all lakes (0.36−0.48 mg·L^{-1}). However, in NR1 and NR2, 3 and 2%, respectively, of this biomass is contributed by Cladocera and the remainder by cyclopoids and *Diaptomus* spp. In MY1, Cladocera are absent and in MY2

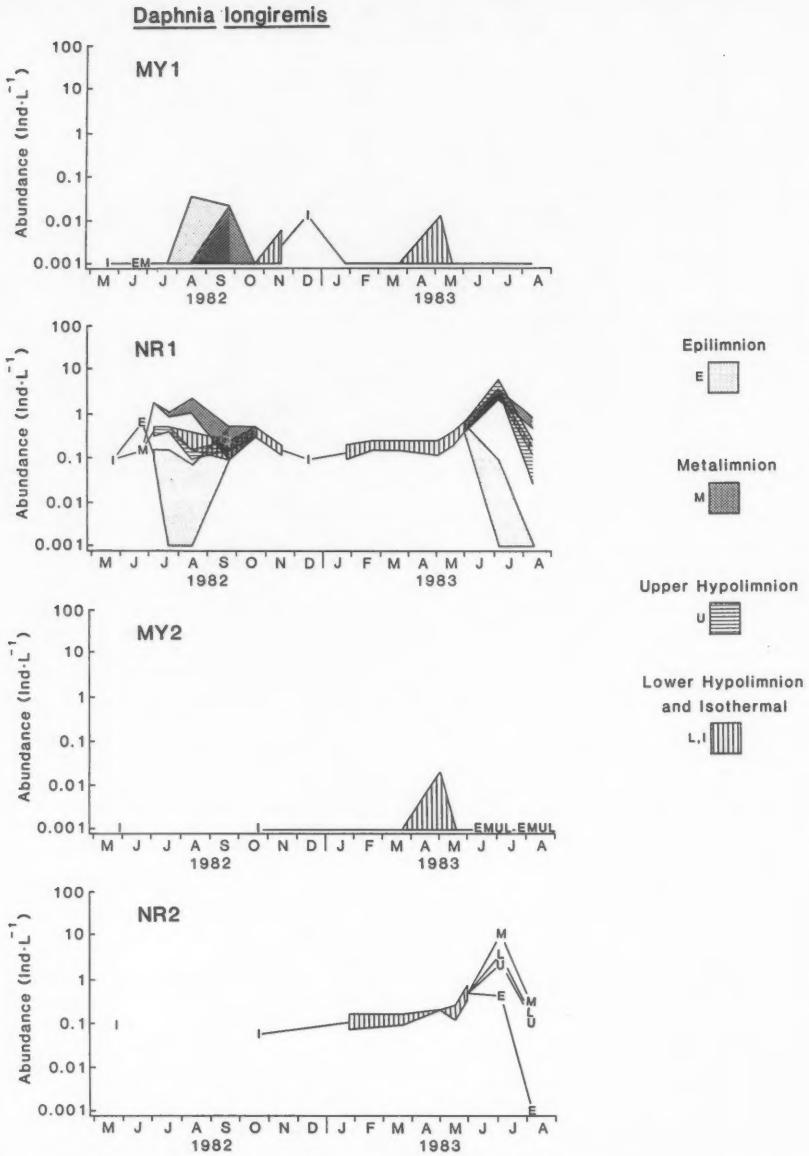


FIG. 4. Seasonal abundance of *Daphnia longiremis*. Shaded regions denote the range in density for three replicate tows. Single lines or letters represent a single tow.

they make up only 0.1% of the plankton biomass. IN MY1 and MY2, 61 and 17%, respectively, of the remainder is contributed by *Mysis*.

Discussion

Nonmysid Influences

Inoculation, by glaciation, of some lakes with *Mysis* and other glacial opportunists provides a "natural experiment" to test the impact of *Mysis* predation on zooplankton communities. However, this experiment is not well controlled; nonpredatory influences such as water chemistry and lake productivity must be considered. Because most nonrelict lakes drain into relict lakes of lower elevation, the latter tend to have the same chemical constituents as the nonrelict lakes. Additional evidence against a chemical cause of the lower abundances of *D. sanguineus*, *D. longiremis*, and *Eubosmina* in lakes with *Mysis* is that all have been observed in these lakes at low densities. These animals most likely coexist at low densities with *Mysis* and are not occasional "immigrants" which would be difficult to detect by net sampling.

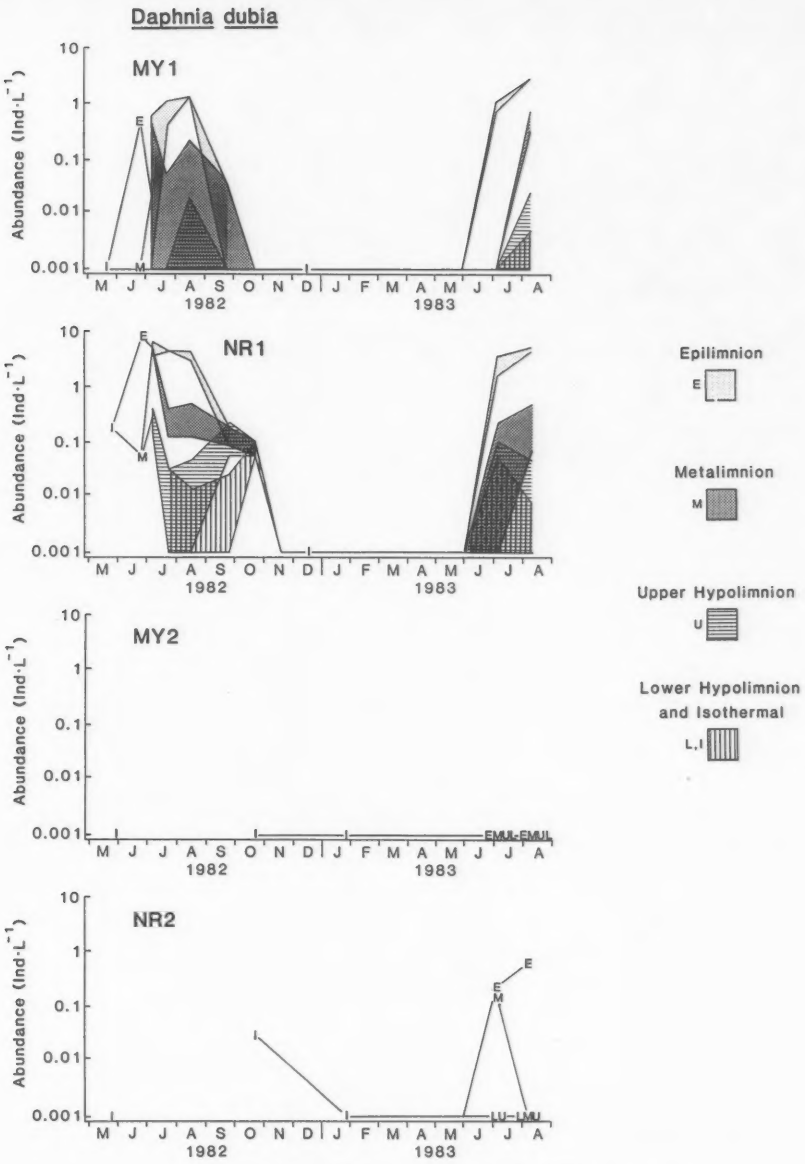


FIG. 5. Seasonal abundance of *Daphnia dubia*.

Indicators of lake productivity have been correlated with zooplankton community types in the study region (Sprules 1977). However, the small range in nutrient parameters (chlorophyll *a*, TN, and TP) indicates that variations in productivity between lake pairs are small, and probably cannot account for differences in the abundance of zooplankton between relict and nonrelict lakes. In addition, comparisons across lake pairs give chemical differences as great as those found within lake pairs. Considering that community differences occurring with the MY and NR lakes are less than community differences between the MY and NR lakes (Fig. 9) leads us to conclude that nonpredatory influences do not seem to account for the observed distribution of zooplankton.

Epischura and other large diaptomids will prey on bosminids and small diaptomids (Kerfoot 1980; Wong 1981), and cyclopoids may be important predators of large, slow-moving rotifers and Cladocera (Li and Li 1979; Williamson and Gilbert 1980; Brandl and Fernando 1981). However, these predators are not likely the cause of low cladoceran densities because cyclopoid densities are higher in the epilimnion, hypolimnion, and during isothermal conditions in NR1 (Table 4) than in MY1. Similar trends of increased Cladocera and cyclopoids in lakes without *Mysis* are also evident from spring survey data (Fig. 3). In addition, predaceous *Epischura* have similar densi-

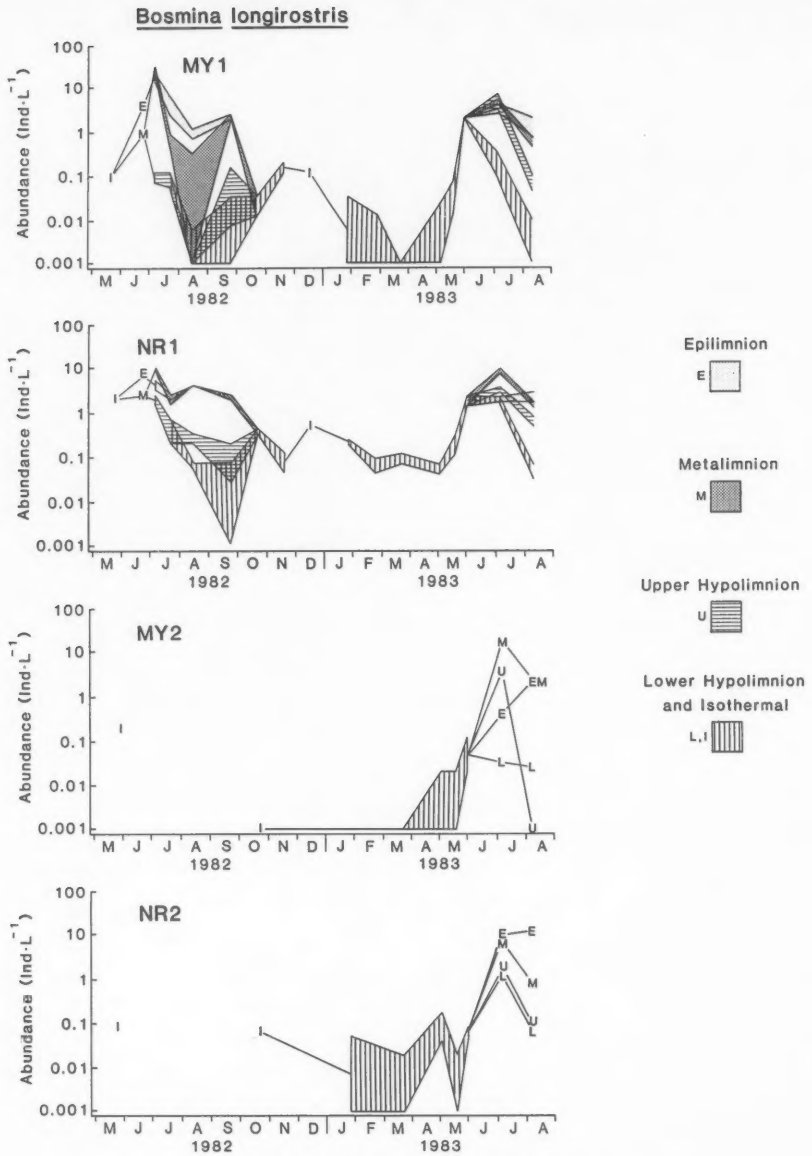


FIG. 6. Seasonal abundance of *Bosmina longirostris*.

ties in both lake types. Because predaceous cladocerans such as *Leptodora* and *Polyphemus* are confined to warm summer epilimnetic waters (Karabin 1974; Butorina 1963), their influence on prey abundances could not be mistaken for that caused by mysids.

Three predators that also occur in Lakes MY1, MY3, and MY5 are the glacial opportunists (*Senecella, Limnocalanus;* and *D. sicilis*). Both *Senecella* and *Limnocalanus* can be very abundant in hypolimnetic strata and during isothermal conditions (Fig. 2). As well, predation rates for *Senecella* and *Limnocalanus* show that their greatest influence will be on copepods, rotifers, and to a lesser extent, hypolimnetic Cladocera (Nero and Sprules 1986). However, cladoceran densities are similarly low in lakes MY1, MY2, and MY4, yet the latter two lakes have neither *Senecella* nor *Limnocalanus*. Therefore, predation by *Senecella* and *Limnocalanus* alone cannot account for the exclusion of Cladocera during isothermal conditions and in hypolimnetic strata. *Limnocalanus* may only be responsible for reduced hypolimnetic densities of copepods and rotifers (Nero and Sprules 1986). Densities of water mites (Hydracarina) and *C. punctipennis* are extremely low, far less than required to influence zooplankton (Riessen 1982; Pastorok 1980).

Obvious vertebrate planktivores, lake whitefish (*Coregonus*

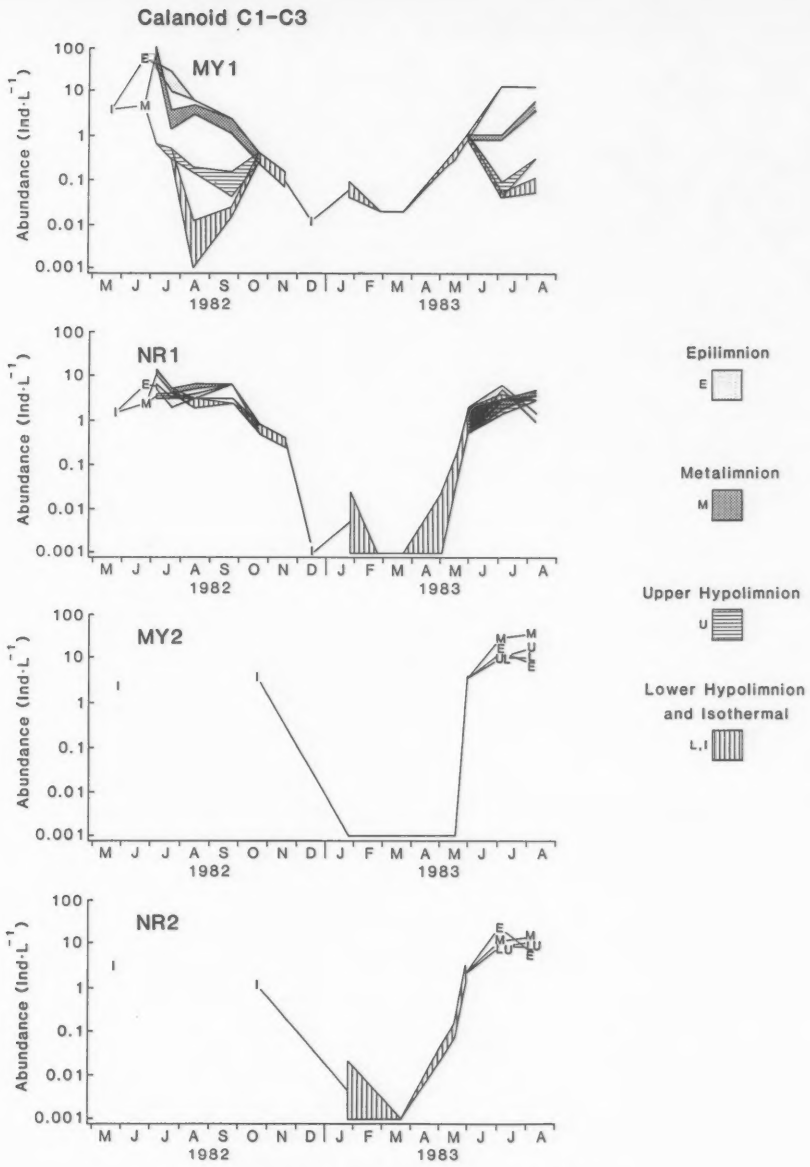


FIG. 7. Seasonal abundance of calanoid copepodites 1–3.

clupeaformis) or lake herring (*Coregonus artedii*) (Scott and Crossman 1973), occur in all our study lakes and they have equal densities in MY1 and NR1, based on echo survey results. These planktivores may explain the absence of large *D. pulex* (Brooks and Dodson 1965), but are not sufficient to explain differences in plankton abundance and composition between MY1 and NR1 or MY2 and NR2. Rainbow smelt (*Osmerus mordax*), present in MY1 only, are not considered a major planktivore (Lane 1979). Members of other fish families are present in all the lakes, but are generally only planktivorous for the first 2–3 wk of their life, during early summer (Scott and Crossman 1973; Keast 1980).

Differences Attributed to Mysids

Most differences are consistent between lake pairs and lend support to the hypothesis that they are caused by *Mysis* predation. This conclusion is supported by low abundances in *Mysis* lakes of those zooplankton species considered most vulnerable to *Mysis*.

Average areal densities of *Mysis* below the thermocline in MY1 and MY2 in early summer (602 and 284 Ind·m^{-2}, respectively) are typical of other Precambrian shield lakes (91–595 Ind·m^{-2}, Nero and Schindler 1983). For introduced populations of *Mysis* at similar densities (100–1980 Ind·m^{-2}),

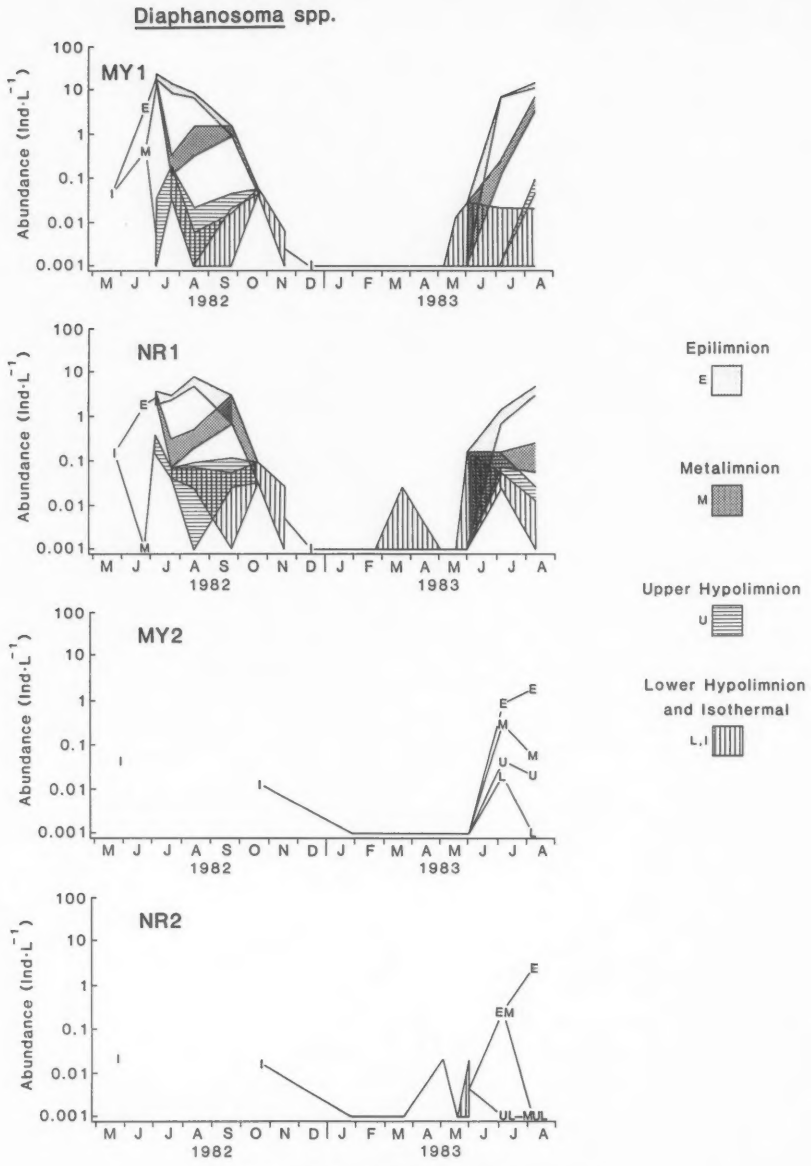


FIG. 8. Seasonal abundance of *Diaphanosoma* spp.

declines in Cladocera have also been reported (Morgan et al. 1981; Reiman and Falter 1981).

Overall species differences between *Mysis* and non-*Mysis* lakes we studied and trends in the data of Roff et al. (1981) reflect the prey preferences of *Mysis* and the results of *Mysis* introductions. *Mysis* exhibit higher predation rates on Cladocera (Bowers and Vanderploeg 1982; Ramcharan et al. 1985), and at least one or a number of cladocerans have declined in abundance following *Mysis* introductions (Goldman et al. 1979; Kinsten and Olsen 1981; Langeland 1981; Morgan et al. 1981). These changes match the low numbers of Cladocera associated with *Mysis* in our survey lakes. As well, two hypolimnetic Cladocera, *D. longiremis* and *Eubosmina*, and two other Cladocera (*D. dubia* and *Holopedium*), were negatively associated with *Mysis* in the Roff et al. (1981) data.

In a study of a natural pair of *Mysis* and non-*Mysis* lakes, Anderson (1977) has shown that *Daphnia* sp. and *Bosmina* sp. abundances are inversely related to *Mysis* densities. Another mysid, *Neomysis mercedis*, has been shown to have excluded *Daphnia* sp. from Lake Washington (Murtaugh 1981a).

For Cladocera, "post-contact" defences against mysids are of limited usefulness (Murtaugh 1981b), especially because of the large size differences between mysids and these prey. However, for copepods, large body size and a concomitant faster

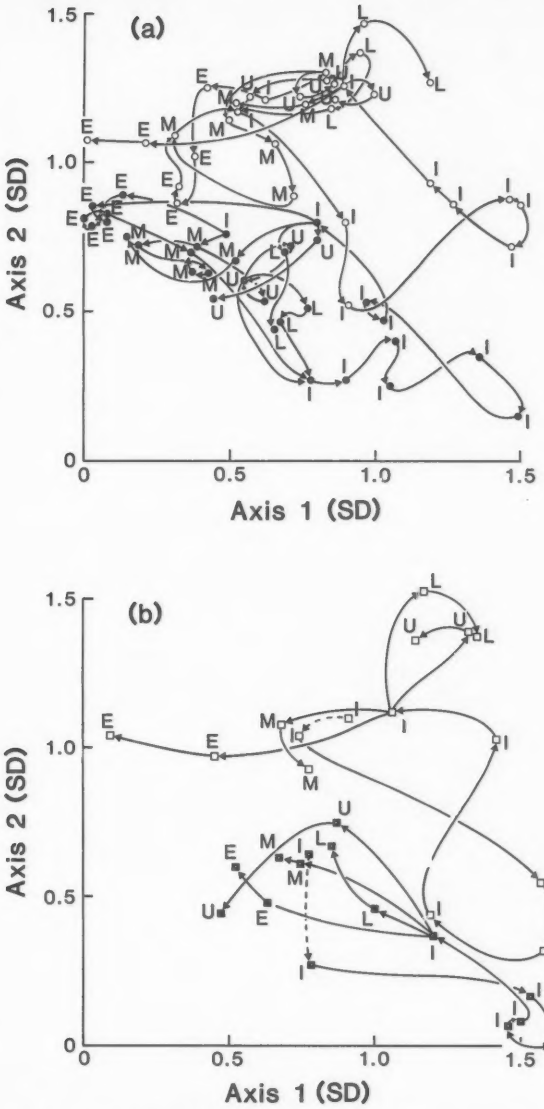


FIG. 9. (a) Ordination by DCA of isothermal (I), epilimnetic (E), metalimnetic (M), upper hypolimnetic (U), and lower hypolimnetic (L) samples from MY1 (●) and NR1 (○) on a species space composed of 20 common zooplankton species. Arrows connect samples in chronological order with disjunct sequences reflecting gaps in sampling. Axes are in units of standard deviation. (b) As in Fig. 9a for MY2 (■) and NR2 (□).

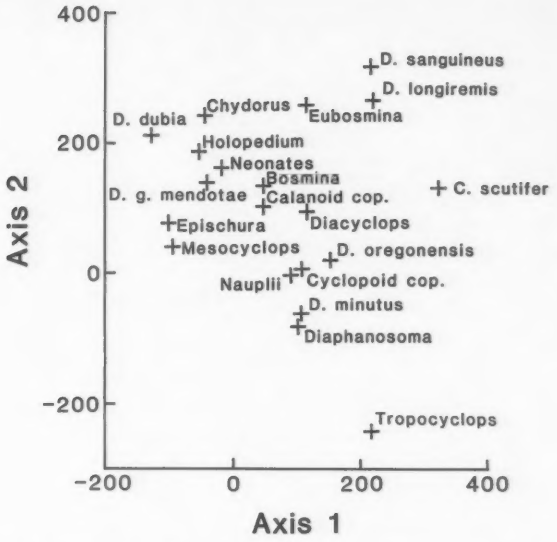


FIG. 10. Simultaneous ordination of 20 common zooplankton species in the sample space depicted in Fig. 9 by DCA. Axes units are arbitrary.

escape speed may be a good "pre-contact" defence against mysids (Ramcharan et al. 1985). Of interest are the large and fast hypolimnetic copepods *Limnocalanus*, *Senecella*, and *D. sicilis*, all of which usually co-occur with *Mysis*.

In addition to species for which *Mysis* have higher predation rates, the vertical distribution of prey species is important in determining effects of *Mysis* predation on populations. Lakes with *Mysis* (MY1 and MY2) lack the hypolimnetic Cladocera *D. longiremis* and *Eubosmina*. Data of Roff et al. (1981) show the same relationship. Epilimnetic Cladocera such as *Bosmina* and *Diaphanosoma* are abundant in epilimnia of lakes containing *Mysis*. During early spring before *Mysis* are excluded from the epilimnion these lakes lack all Cladocera. Clearly, species with a preference for the epilimnion are less vulnerable to *Mysis*.

Warm water refugia from *Mysis* have been recognized for a number of Cladocera. *Bosmina*, *D. g. mendotae*, *Daphnia thorata*, and other Cladocera all occur in the epilimnion during late summer and fall in Donner and Fallen Leaf lakes (Morgan et al. 1981), Pend Orielle Lake (Rieman and Falter 1981), and Kootenay Lake (Zyblut 1970; Daley et al. 1981).

Some Cladocera may avoid *Mysis* through their diurnal migratory cycles. In Lake Michigan some Cladocera migrate vertically into the epilimnion at night, thereby avoiding *Mysis* (Bowers and Vanderploeg 1982). The extent to which short (<5 m) migrations occur in natural relict lakes studied here is not known. In addition, mysids may make short feeding excursions into the warm epilimnion at night (Murtaugh 1981a). In small stratified lakes, thermoclines can be very steep. Only a short 0.5-m excursion would be sufficient to bring *Mysis* into contact with epilimnetic prey. Information on the short-term temperature tolerance of *Mysis* combined with detailed migratory behavior would provide valuable insights into this feeding behavior.

Lake productivity now appears to be an important determinant of the extent to which *Mysis* can influence zooplankton populations. In low-productivity lakes such as Lake Tahoe, Cladocera subsist (Goldman et al. 1979). Increased death rates caused by *Mysis* are sufficient to cause major population declines (Goldman et al. 1979). In the more productive Emerald Bay of Lake Tahoe, and in Donner and Fallen Leaf lakes, the influence of *Mysis* is not as great, presumably due to higher birth rates among the Cladocera (Morgan et al. 1981; Goldman et al. 1979). In the moderately oligotrophic MY1 and MY2 (average summer TP 9 $\mu g \cdot L^{-1}$), higher productivity and warm

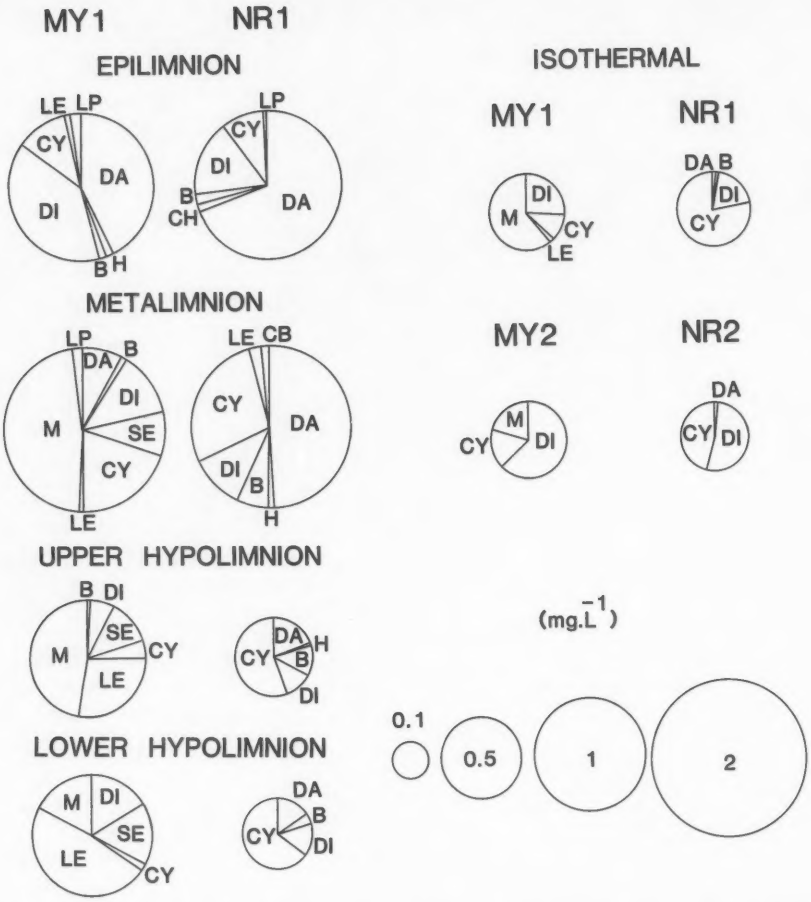


FIG. 11. Pie charts of taxonomic group contribution to biomass for MY1 and NR1 during stratification (left side) and Lakes MY1, NR1, MY2, and NR2 during isothermal conditions (right side). Groups (clockwise): DA, daphnids; CH, *Chydorus*; H, *Holopedium*; B, bosminids; DI, *Diaptomus*; SE, *Senecella*; CY, cyclopoids; LE, *Limnocalanus* and *Epischura*; M, *Mysis*; LP, *Leptodora*; CB, *Chaoborus*. Circle area is proportional to total biomass.

water refuge in the epilimnion may contribute to the coexistence of species with *Mysis* during midsummer. Most Precambrian shield lakes are more oligotrophic than MY1 and MY2 (typical epilimnetic TP values of 2−9 $\mu g \cdot L^{-1}$; Prokopowich 1979), and the influence of *Mysis* on Cladocera is probably greater than that observed in MY1 and MY2.

Food limitation and competition between herbivorous Cladocera has been recognized as an important determinant of species composition and abundance, with the outcome dependent on predation on one of the competitors (Sprules 1972; Smith and Cooper 1982; DeMott 1983). With *Mysis*, less vulnerable Cladocera may experience competitive release as their more vulnerable competitors are eliminated. *Diaphanosoma* may be such a species. It is likely a competitor of *Daphnia*, but is less vulnerable to *Mysis* because of its faster swimming speed (Swift and Fedorenko 1975) and concomitant escape ability. Field evidence supports this hypothesis. *Diaphanosoma* is positively associated with *Mysis* in MY1, MY2, and in Kootenay Lake (Zyblut 1970; Daley et al. 1981). Rieman and Falter (1981) noted an increase in *Diaphanosoma* in Pend Oreille Lake following establishment of *Mysis*. Finally, the positive correlation of *Diaphanosoma* with *Mysis* in the Roff et al. (1981) data indicates that this trend is widespread throughout a large number of lakes. However, estimates of in situ feeding rates indicate that *Diaphanosoma* is as susceptible as other Cladocera (Nero and Sprules 1986). One alternative is that this species may undergo short-distance vertical migrations (1−2 m) into the epilimnion at night.

Mysis appear to influence zooplankton communities of oligotrophic Precambrian shield lakes, and are attributed with causing low densities of hypolimnetic Cladocera. These species are vulnerable because of their hypolimnetic distributions and high vulnerability to *Mysis* feeding. Some Cladocera resist *Mysis* predation, but detailed predation studies of *Mysis* feeding on presumably less susceptible Cladocera (*Diaphanosoma* sp. and *Bosmina*) are still required to elucidate the mechanisms involved. The presence of *Mysis* has implications for fisheries. A scarcity of hypolimnetic Cladocera in lakes with *Mysis* may have a negative influence on recruitment of cold water fish, far greater than any benefits juvenile fish receive

through the use of *Mysis* as a food source. Detailed experimental data on the exact costs to cold water fish feeding in lakes which contain *Mysis* are required.

Acknowledgments

We thank W. Norwood and J. Bendell for assistance in the field and T. Carleton, Department of Botany, University of Toronto, who provided a computer program for detrended correspondence analysis. D. C. Lasenby and an anonymous reviewer provided suggestions to help improve the manuscript. This research was funded by operating grants from the Natural Sciences and Engineering Research Council of Canada and the Canadian National Sportsmen's Fund awarded to W. G. Sprules.

References

AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1975. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, DC. 1193 p.

ANDERSON, R. S. 1977. Rotifer populations in mountain lakes relative to fish and species of copepods present. Ergebn. Limnol. 8: 130–134.

BEETON, A. M. 1960. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. J. Fish. Res. Board Can. 17: 517–539.

BOWERS, J. A., AND H. A. VANDERPLOEG. 1982. *In situ* predatory behavior of *Mysis relicta* in Lake Michigan. Hydrobiologia 93: 121–131.

BRANDL, Z., AND C. H. FERNANDO. 1981. The impact of predation by cyclopoid copepods on zooplankton. Verh. Int. Ver. Limnol. 21: 1573–1577.

BRANDLOVA, J., Z. BRANDL, AND C. H. FERNANDO. 1972. The Cladocera of Ontario with remarks on some species and distribution. Can. J. Zool. 50: 1373–1403.

BROOK, A. J., AND W. B. WOODWARD. 1956. Some observations on the effects of water inflow and outflow on the plankton of small lakes. J. Anim. Ecol. 25: 22–35.

BROOKS, J. R., AND S. I. DODSON. 1965. Predation, body size and composition of zooplankton. Science (Wash., DC) 150: 28–35.

BUTORINA, L. G. 1963. Some data on the distribution and life cycle of *Polyphemus pediculus*. Tr. Inst. Biol. Vnutr. Vod. 6: 143–152. (Translated from Russian by the Freshwater Biological Association)

CARTER, J. C. H., M. J. DADSWELL, J. C. ROFF, AND W. G. SPRULES. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. Can. J. Zool. 58: 1355–1387.

CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley & Sons Inc., Toronto, Ont. 462 p.

DADSWELL, M. J. 1974. Distribution ecology and postglacial dispersal of certain crustaceans and fishes in eastern North America. Nat. Mus. Can. Publ. Zool. 11: 110 p.

DALEY, R. J., E. C. CARMACK, C. B. J. GRAY, C. H. PHARO, S. JASPER, AND R. C. WIEGAND. 1981. The effects of upstream impoundments on the limnology of Kootenay Lake, B.C. Nat. Water Res. Inst. Sci. Ser. 117: 242 p.

DE BERNARDI, R. 1984. Methods for the estimation of zooplankton abundance, p. 59–86. *In* J. A. Downing and F. H. Rigler [ed.] A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific Publications, Boston, MA.

DEEVEY, E. S., AND G. B. DEEVEY. 1971. The American species of *Eubosmina seligo* (Crustacea, Cladocera). Limnol. Oceanogr. 16: 201–218.

DEMOTT, W. R. 1983. Seasonal succession in a natural *Daphnia* assemblage. Ecol. Monogr. 53: 321–340.

DILLON, P. J., D. S. JEFFRIES, W. SNYDER, R. REID, N. D. YAN, D. EVANS, J. MOSS, AND W. A. SCHEIDER. 1978. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. 35: 809–815.

FURST, M. 1981. Results of introductions of new fish food organisms into Swedish lakes. Rep. Inst. Freshwater Res. Drottningholm 59: 3–47.

GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, NY. 298 p.

GOLDMAN, C. R., M. D. MORGAN, S. T. THRELKELD, AND N. ANGELI. 1979. A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California–Nevada. Limnol. Oceanogr. 24: 289–297.

GOSHO, M. E. 1975. The introduction of *Mysis relicta* into freshwater lakes. Fish. Res. Inst. College Fish. Univ. Wash. Circ. No. 75: 65 p.

GROSSNICKLE, N. E. 1978. The herbivorous and predaceous habits of *Mysis relicta* in Lake Michigan. Ph.D. thesis, University of Wisconsin, Milwaukee, WI. 107 p.

KARABIN, A. 1974. Studies on the predatory role of the Cladoceran, *Leptodora kindtii* (Focke), in secondary production of two lakes with different trophy. Ekol. Pol. 22: 295–310.

KEAST, A. 1980. Food and feeding relationships of young fish in the first weeks after the beginning of exogenous feeding in Lake Opinicon, Ontario. Environ. Biol. Fishes 5: 305–314.

KELSO, J. R. M., AND C. K. MINNS. 1975. Summer distribution of the nearshore fish community near a thermal generating station as determined by acoustic census. J. Fish. Res. Board Can. 32: 1409–1418.

KELSO, J. R. M., E. E. PICKETT, AND R. G. DOWD. 1974. A digital echo-counting system used in determining abundance of freshwater pelagic fish in relation to depth. J. Fish. Res. Board Can. 31: 1101–1104.

KERFOOT, W. C. [ED.] 1980. Evolution and ecology of zooplankton communities. University Press of New England, Hanover, NH. 793 p.

KINSTEN, B., AND P. OLSEN. 1981. Impact of *Mysis relicta* Loven introduction on the plankton of two mountain lakes, Sweden. Rep. Inst. Freshwater Res. Drottningholm 59: 64–74.

LANE, P. A. 1979. Vertebrate and invertebrate predation intensity on freshwater zooplankton communities. Nature (Lond.) 280: 391–393.

LANGELAND, A. 1981. Decreased zooplankton density in two Norwegian lakes caused by predation of recently introduced *Mysis relicta*. Verh. Int. Ver. Limnol. 21: 926–937.

LASENBY, D. C., AND M. FURST. 1981. Feeding of *Mysis relicta* Loven on macrozooplankton. Rep. Inst. Freshwater Res. Drottningholm 59: 75–80.

LASENBY, D. C., AND R. R. LANGFORD. 1973. Feeding and assimilation of *Mysis relicta*. Limnol. Oceanogr. 18: 280–285.

LI, J. L., AND H. W. LI. 1979. Species-specific factors affecting predator–prey interactions of the copepod *Acanthocyclops vernalis* with its natural prey. Limnol. Oceanogr. 24: 613–626.

MORGAN, M. D., C. R. GOLDMAN, AND R. C. RICHARDS. 1981. Impact of introduced populations of *Mysis relicta* on zooplankton in oligotrophic subalpine lakes. Verh. Int. Ver. Limnol. 21: 339–345.

MORGAN, M. D., AND S. T. THRELKELD. 1982. Size dependent horizontal migration of *Mysis relicta*. Hydrobiologia 93: 63–68.

MORGAN, M. D., S. T. THRELKELD, AND C. R. GOLDMAN. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. J. Fish. Res. Board Can. 35: 1572–1579.

MURTAUGH, P. A. 1981a. Selective predation by *Neomysis mercedis* in Lake Washington. Limnol. Oceanogr. 26: 445–453.

1981b. Size-selective predation on *Daphnia* by *Neomysis mercedis*. Ecology 62: 894–900.

1983. Mysid life history and seasonal variation in predation pressure on zooplankton. Can. J. Fish. Aquat. Sci. 40: 1968–1974.

NATIONAL RESEARCH COUNCIL OF CANADA. 1981. Acidification in the Canadian aquatic environment: scientific criteria for assessing the effects of acidic deposition on aquatic ecosystems. Natl. Res. Counc. Can. Assoc. Comm. Sci. Criter. Environ. Qual. Publ. 18475: 369 p.

NERO, R. W. 1982. A description of three nets suitable for estimating the abundance of *Mysis relicta*. Can. Tech. Rep. Fish. Aquat. Sci. 1046: iv + 8 p.

NERO, R. W., AND I. J. DAVIES. 1982. Comparison of two sampling methods for estimating the abundance and distribution of *Mysis relicta*. Can. J. Fish. Aquat. Sci. 39: 349–355.

NERO, R. W., AND D. W. SCHINDLER. 1983. Decline of *Mysis relicta* during the acidification of Lake 223. Can. J. Fish. Aquat. Sci. 40: 1905–1911.

NERO, R. W., AND W. G. SPRULES. 1986. Predation by three glacial opportunists on natural zooplankton communities. Can. J. Zool. 64. (In press).

ONTARIO MINISTRY OF THE ENVIRONMENT. 1981. Acid sensitivity survey of lakes in Ontario. Ontario Ministry of the Environment, Toronto, Ont. iv + 137 p.

PALOHEIMO, J. E., AND A. P. ZIMMERMAN. 1983. Factors influencing phosphorus–phytoplankton relationships. Can. J. Fish. Aquat. Sci. 40: 1804–1812.

PASTOROK, R. A. 1980. Selection of prey by *Chaoborus* larvae: a review and new evidence for behavioral flexibility, p. 538–554. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. University Press of New England, Hanover, NH.

PATALAS, K. 1971. Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 231–244.

PREST, W. K. 1970. Quaternary geology of Canada, p. 676–764. *In* R. J. W. Douglas [ed.] Geology and economic minerals of Canada. Geol. Surv.

Can. Econ. Geol. Rep.

PROKOPOWICH, J. 1979. Chemical characterization of epilimnion waters in the Experimental Lakes Area, northwestern Ontario. Can. Fish. Mar. Serv. Tech. Rep. 873: iv + 41 p.

RAMCHARAN, C. W., W. G. SPRULES, AND R. W. NERO. 1985. Notes on the tactile feeding behaviour of *Mysis relicta* Loven (Malacostraca: Mysidacea). Verh. Int. Ver. Limnol. 22: 3215–3219.

RAY, A. A. [ED.] 1982. SAS user's guide: statistics. Statistical Analysis System Institute Incorporated, Cary, NC. 584 p.

RIEMAN, B. E., AND C. M. FALTER. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Trans. Am. Fish. Soc. 110: 613–620.

RIESSEN, H. P. 1982. Predatory behavior and prey selectivity of the pelagic water mite *Piona constricta*. Can. J. Fish. Aquat. Sci. 39: 1569–1579.

ROFF, J. C., W. G. SPRULES, J. C. H. CARTER, AND M. J. DADSWELL. 1981. The structure of crustacean zooplankton communities in glaciated eastern North America. Can. J. Fish. Aquat. Sci. 38: 1428–1437.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184: 966 p.

SEGERSTRALE, S. G. 1962. The immigration and prehistory of the glacial relicts of Eurasia and North America. A survey and discussion of modern views. Int. Rev. Gesamten Hydrobiol. 47: 1–25.

SMITH, D. W., AND S. D. COOPER. 1982. Competition among Cladocera. Ecology 63: 1004–1015.

SMITH, K., AND C. H. FERNANDO. 1978. A guide to the freshwater calanoid and cyclopoid copepod crustacea of Ontario. Univ. Waterloo Biol. Ser. 18: 74 p.

SPRULES, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375–386.

——— 1977. Crustacean zooplankton communities as indicators of limnological conditions: an approach using principal component analysis. J. Fish. Res. Board Can. 34: 962–975.

SPRULES, W. G., L. B. HOLTBY, AND G. GRIGGS. 1981. A microcomputer measuring device for biological research. Can. J. Zool. 59: 1611–1614.

STRASKRABA, M. 1980. The effects of physical variables on freshwater production: analyses based on models, p. 13–84. *In* E.D. LeCren and R. H. Lowe-McConnell [ed.] The functioning of freshwater ecosystems. Cambridge University Press, New York, NY.

SWIFT, M. C., AND A. Y. FEDORENKO. 1975. Some aspects of prey capture by *Chaoborus* larvae. Limnol. Oceanogr. 20: 418–425.

THRELKELD, S. T. 1981. The recolonization of Lake Tahoe by *Bosmina longirostris*: evaluating the importance of reduced *Mysis relicta* populations. Limnol. Oceanogr. 26: 433–444.

WILLIAMSON, C. E., AND J. J. GILBERT. 1980. Variation among zooplankton predators: the potential of *Asplanchna*, *Mesocyclops*, and *Cyclops* to attack, capture, and eat various rotifer prey, p. 509–517. *In* W. C. Kerfoot [ed.] Evolution and ecology of zooplankton communities. University Press of New England, Hanover, NH.

WONG, C. K. 1981. Predatory feeding behavior of *Epischura lacustris* (Copepoda, Calanoida) and prey defence. Can. J. Fish. Aquat. Sci. 38: 275–279.

YAN, N. D., R. W. NERO, W. KELLER, AND D. C. LASENBY. 1985. Are *Chaoborus* larvae more abundant in acidified than in non-acidified lakes in central Canada? Holarct. Ecol. 8: 93–99.

ZYBLUT, E. R. 1970. Long-term changes in the limnology and macrozooplankton of a large British Columbia lake. J. Fish. Res. Board Can. 27: 1239–1250.

Influence of Salmonine Predation and Weather on Long-Term Water Quality Trends in Lake Michigan[1]

Donald Scavia and Gary L. Fahnenstiel

Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, MI 48104, USA

Marlene S. Evans and David J. Jude

Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA

and John T. Lehman

Biological Sciences and Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA

Scavia, D., G. L. Fahnenstiel, M. S. Evans, D. J. Jude, and J. T. Lehman. 1986. Influence of salmonine predation and weather on long-term water quality in Lake Michigan. Can. J. Fish. Aquat. Sci. 43: 435–443.

Trends in Lake Michigan water quality over 1975–84 appear to reflect reduced nutrient loadings as indicated by gradual declines in spring total phosphorus (TP) and summer epilimnetic chlorophyll *a* (Chl *a*). Deviations from these trends during 1977 and 1983–84 were apparently caused by abiotic and biotic factors, respectively. Prolonged ice cover during 1977 decreased sediment resuspension resulting in lower TP, reduced Chl *a* levels, and increased water clarity. A similar dramatic result occurred in 1983 and to a lesser extent in 1984, but via a different mechanism. Burgeoning populations of stocked salmonines reduced populations of the planktivorous alewife (*Alosa pseudoharengus*), which allowed large *Daphnia* to flourish. Because the *Daphnia* are more voracious and nonselective grazers than the formerly dominant calanoid copepods, they reduced seston concentrations, causing dramatic increases in Secchi disk transparency. These exceptions demonstrate the far-reaching consequences that unusual weather conditions and fish management practices may have on water quality indicators.

Les tendances de la qualité de l'eau du lac Michigan entre 1975 et 1984 reflètent la réduction des charges en matières nutritives indiquée par des déclins graduels de la teneur en phosphore total (PT) au printemps et en chlorophylle *a* (Chl *a*) de l'épilimnion en été. Les écarts aux tendances notés en 1977 et en 1983–1984 semblent s'expliquer respectivement par des facteurs abiotiques et biotiques. La présence de glace pendant une plus longue période en 1977 a été la cause d'une moins grande resuspension des sédiments, qui s'est traduite par des teneurs en PT et Chl *a* moins importantes et par une augmentation de la transparence des eaux. Un effet similaire très prononcé a été noté en 1983 et, dans une moindre mesure, en 1984, mais le mécanisme était différent. Les populations en expansion des salmonines d'élevage introduits dans le lac ont provoqué une réduction des populations du gaspareau planctivore (*Alosa pseudoharengus*), ce qui a permis aux grosses *Daphnia* de devenir plus abondantes. Les *Daphnia*, brouteurs non sélectifs plus voraces que les copépodes calanoïdes qui dominaient auparavant, ont réduit les concentrations de seston, ce qui s'est traduit par des augmentations très importantes de la transparence des eaux déterminée au disque de Secchi. Ces exceptions montrent la grande portée des effets que peuvent avoir des conditions météorologiques inhabituelles et certaines pratiques de gestion du poisson sur les indicateurs de la qualité de l'eau.

Received June 5, 1985
Accepted October 21, 1985
(J8279)

Reçu le 5 juin 1985
Accepté le 21 octobre 1985

It can be difficult to assess a water body's response to altered driving forces. This is especially true for very large water bodies with long residence times. Physical, chemical, and biological forces influence lake trophic status. Physical forces influence lakes through control of their heat content, water movements, and hydraulic loads (Boyce 1974; Denman and Powell 1984). Chemical factors, such as nutrient and organic overenrichment and toxins, also affect water quality and ecosystem structure. More recently, biological factors have been recognized as potentially important in determining the trophic condition of a lake (Hrbáček 1962; Shapiro et al. 1975; Lampert 1978; Edmondson and Litt 1982; Carpenter and Kitchell 1984). Some of these forces can be controlled or modified through human intervention. Most notable of these actions is nutrient abatement, which may include reduction of nutrient loads by sewage diversion or by treatment. Biological control can be implemented through fish manipulations (e.g. Stenson et al. 1978; Shapiro and Wright 1983). Physical alterations are more difficult to accomplish than biological or chemical alterations; however, in some cases artificial aeration and mixing have been implemented (see references in McQueen et al. 1984). It can also be difficult to separate responses of one

[1]Contribution No. 464, Great Lakes Environmental Research Laboratory, NOAA, and Contribution No. 435, Great Lakes Research Division, The University of Michigan.

portion of the ecosystem due to anthropogenic alterations in the watershed from those that are either natural (e.g. meteorological events) or directed at a seemingly distant portion of the ecosystem.

The Laurentian Great Lakes have been the subject of a massive program designed to improve water quality of the lower, more eutrophic lakes — Lakes Erie and Ontario — and to protect the current status of the upper, less productive lakes — Lakes Superior, Huron, and Michigan (Slater and Bangay 1980). The effort has focused largely on reducing the supply of phosphorus (Schelske 1979). This strategy of eutrophication control by nutrient manipulation appears to have improved water quality as measured by the extent of hypolimnetic anoxia, changes in total phosphorus (TP) concentrations, chlorophyll *a* (Chl *a*) concentrations, water transparency, and phytoplankton species composition in Lake Ontario, Lake Erie, Saginaw Bay, and the southern portion of Lake Huron (e.g. International Joint Commission 1984; Dobson 1981).

These lakes are also affected by other management activities (Sonzogni et al. 1983). For example, Lake Michigan is one of the lakes that is managed at the top of the food web through an aggressive salmonine stocking program begun in the mid-1960's. This successful stocking program, continued control of the salmonine predator, the sea lamprey (*Petromyzon marinus*), and largely unsuccessful natural reproduction of stocked lake trout (*Salvelinus namaycush*) (Eshenroder et al. 1984) have produced "a management-dependent system dominated by exotic fish" (Walters et al. 1980; Stewart et al. 1981). Thus, Lake Michigan, the world's fourth largest freshwater lake, sustains an ecosystem that is forced anthropogenically from above (fish stocking) as well as from below (phosphorus control). These anthropogenic forces are superimposed upon natural forces, such as meteorological conditions.

To assess overall trend in water quality, we have analyzed Lake Michigan data accumulated from a region offshore of Grand Haven, Michigan, over the past 10 yr. In general, we found a slight improvement in water quality over the 10-yr period. However, we also detected two periods of dramatic deviation from the overall trend. Certain symptoms of these "outlier" years are similar: lower Chl *a* and clearer water. The suspected causes of these symptoms are dramatically different; one is physical and stochastic, the other is ecological and may be a serendipitous result of changes in fish populations. The data we present below are consistent with two hypotheses concerning these periods of deviation. (1) Severe ice cover in winter 1977 resulted in reduced TP concentration in spring. We suggest that reduced spring TP was manifest further as lower Chl *a* concentrations and clearer water in summer. (2) Cascading effects (Carpenter and Kitchell 1984) of fish manipulations at the top of Lake Michigan's food web have induced changes in planktivorous fish, zooplankton species composition, Chl *a* concentrations, and finally water clarity. Below we outline evidence, primarily from Lake Michigan, that support these hypotheses.

Methods

Data used in this work have come from various sources. Most were based on samples taken from stations at 70- to 100-m depths in southeastern Lake Michigan approximately 16–30 km offshore of Grand Haven. Except for 1977, 1982, 1983, and 1984, zooplankton were primarily from an offshore station (40 m depth) approximately 105 km south of Grand Haven (offshore of Bridgman, MI); during those years, collections were also made to the west of Grand Haven.

Total P data are spring values from data files of the Great Lakes Environmental Research Laboratory (GLERL), Rockwell et al. (1980a), EPA Storage and Retrieval System (STORET), and D. Rockwell (Environmental Protection Agency, Chicago, IL). Secchi disk depths are from GLERL data files, Rockwell et al. (1980a), and M. S. Evans and R. A. Moll (University of Michigan, Ann Arbor, MI). Chlorophyll *a* samples were collected on glass fiber filters, ground, extracted in acetone, and processed either fluorometrically or spectrophotometrically (R. A. Moll and GLERL data files) except for Environmental Protection Agency samples (Rockwell et al. 1980a) which were sonicated rather than ground. Data from R. A. Moll for 1977 were from in vivo fluorescence corrected by calibration to extracted samples.

Transmissivity measurements were all taken aboard the R/V *Shenehon* with a submersible transmissometer. Because the path length of the system has varied from 1 m to 25 cm over the 10-yr period, all measurements were converted to 1 m following Beer's law. A Kahlsico, Inc., system with an incandescent light source was used during 1975–81, and was then replaced with a Sea Tech, Inc., model 25 transmissometer with a light-emitting diode ($\lambda = 660$ μm). We used wavelength-specific extinction coefficients for Lake Michigan water (G. L. Fahnenstiel, unpubl. data) and spectral characteristics of the light sources and detectors for both systems to normalize data. Because detectors from both systems respond fairly uniformly to light of different wavelengths, the ratio (R) of transmissivity measured from a given water mass can be calculated as

$$R = \frac{\sum_i a_{K,i} e^{-k_i}}{\sum_i a_{S,i} e^{-k_i}}$$

where k_i are the extinction coefficients for Lake Michigan and $a_{K,i}$ and $a_{S,i}$ are the fractions of light-energy from the Kahlsico (K) and Sea Tech (S) light sources for each wavelength interval i. The resulting ratio is 1.203 for our instruments used in Lake Michigan water.

The depth of the 1% light level was calculated from extinction coefficients for photosynthetically active radiation (PAR) determined by scalar sensors or by hemispherical (upwelling and downwelling) sensors corrected to scalar estimates following Spigel and Howard-William (1984).

Zooplankton dry weights for 1975–81 were determined from species collected with net hauls from 40 m to the surface (Evans et al. 1980; M. S. Evans, unpubl. data) and individual dry weights as described in Hawkins and Evans (1979). Zooplankton composition for 1983 was determined (J. T. Lehman) from samples pumped through 153-μm-mesh nets. Data for 1984 were again from net hauls from 40 m to the surface (D. Scavia and G. L. Fahnenstiel). Weights for 1982, 1983, and 1984 calculations were based on dry-weight measurements of animals collected in those years. Mean weights were estimated by measuring dry weight of several individuals of the predominant species. *Daphnia pulicaria* mean weight (13.09 μg) was based on a weighted average of large and small individuals. Comparisons between net collections from 40 m to the surface and detailed vertical profiles of discrete, pumped samples in 1977 indicated little bias in dominant crustaceans, except for nauplii and mysids (M. S. Evans, unpubl. data). Data on alewife (*Alosa pseudoharengus*) biomass are from

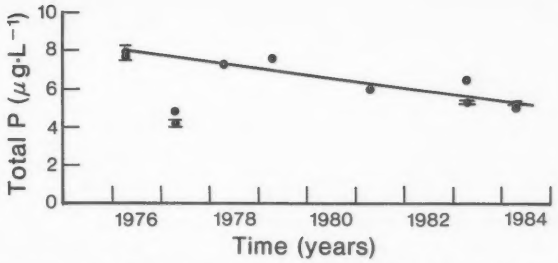


FIG. 1. Total P during spring isothermal conditions for 1976–84. Points represent data from the region off Grand Haven, MI. Bars represent the mean ±1 SE for southern basin stations with depths greater than 80 m.

Wells and Hatch (1984) and L. Wells (Great Lakes Fishery Laboratory, Ann Arbor, MI). These abundance estimates are from bottom trawls taken inshore of the 100-m depth contour in autumn at eight index stations from around the lake and represent adult alewife available for midwater planktivory.

Zooplankton grazing experiments conducted in 1983 followed the method described by Lehman (1980). Chlorophyll-based algal net growth rates were measured in rotating 20-L enclosures containing different amounts of zooplankton and incubated at ambient temperature and light for 24 h. The slope of the algal growth rate versus zooplankton abundance curve represents the filtering rate of the zooplankton community.

One must be cautious when using data from different seasons to evaluate changes over years. For Secchi depth, epilimnetic Chl *a*, and transmissivity we present all data and examine detectable signals, as it was not always possible to calculate meaningful averages. Because timing of the onset of stratification is critical and varies from year to year, we delineate critical periods in Fig. 2 by shading from the onset of stratification in late spring to fall when the thermocline passes 15 m and begins to deepen rapidly. For examination of trends, we considered TP prior to the onset of thermal stratification. Chlorophyll *a*, water clarity, and zooplankton biomass trends are viewed through the window of thermal stratification.

Results and Discussion

Water Quality Trends

Total P

Late winter and early spring TP, generally considered a good indicator of trophic state (e.g. Dillon and Rigler 1974), decreased slowly and systematically from 1975 to 1984 (Fig. 1). These regional data from the isothermal spring period are consistent with data averaged from southern basin stations in 1976, 1977, 1983, and 1984; consequently, at least the southern basin of Lake Michigan has apparently experienced TP reductions. A notable exception to the gradual trend is the outlying datum from 1977, which will be discussed below.

Chlorophyll a

Surface Chl *a* varied seasonally in a somewhat regular pattern each year (Fig. 2a). Algal blooms prior to thermocline development are generally composed of diatom species (Brooks and Torke 1977; Parker et al. 1977; Bartone and Schelske 1982). Once thermal stratification develops, this major bloom sinks from the epilimnion. Under strong stratification during midsummer, a clear water phase is produced by a growth season minimum of Chl *a*, similar to that of several European lakes (Sommer 1984). The end of this phase in early autumn is often signaled by increases in Chl *a* concentration.

Summer Chl *a* minima did not change dramatically over the decade. From relationships developed between spring TP and Chl *a* (which are typical of the Great Lakes), one might expect little observable change in Chl *a* for a 2 $\mu g \cdot L^{-1}$ change in TP. Models by Chapra and Dobson (1981) and Vollenweider et al. (1980) predict, respectively, 0.5 and 0.3 $\mu g \cdot L^{-1}$ changes in summer average Chl *a* over the 10 yr, corresponding to a 2 $\mu g \cdot L^{-1}$ change in TP. However, Chl *a* minima fell below 0.5 $\mu g \cdot L^{-1}$ in 1977 and 1983, which is less than half the typical minimum values in this data set. Reduced Chl *a* concentrations in 1977 and 1983 were also reflected in other indications of a clearer water column.

Water clarity

Secchi disk depth followed systematic patterns each year (Fig. 2b). Typically, there was a minimum prior to stratification corresponding with the spring Chl *a* maximum. This was followed by increased transparency during midsummer and then a subsequent dramatic decrease during late summer – early fall, the latter often associated with calcite precipitation ("whitings"). Ladewski and Stoermer (1973) discussed the dramatic seasonal dynamics of Secchi depth as driven by whitings in 1972 in Lake Michigan, and Strong and Eadie (1978) and B. J. Eadie (GLERL, unpubl. data) reported that whitings are a regular phenomenon in Lake Michigan, Lake Ontario, Lake Erie, and southern Lake Huron. The long-term trend in Secchi depth is toward higher values in general. There are again clear signals that maximum midsummer Secchi depths were deeper in 1977 and 1983 than in other years.

Transmissometer data (Fig. 2c) follow a seasonal pattern similar to that of Secchi depth. Maximum transmissivity of surface waters occurs during midsummer. Lower values before and after this period correspond with the spring algal maxima and deepening of the thermocline or whitings, respectively. The long-term trend in this variable also indicates a general improvement in water clarity. Although not as dramatic, the 1983 signal is consistent with lower Chl *a* concentrations; there were no data available to evaluate the 1977 signal. The most dramatic evidence for the increased water clarity in 1983 comes from the 1% light depth (depth of the photic zone) calculated from measured PAR extinction (Table 1). The depth of 1% light penetration reached 32.8 m in July 1983, which corresponds to an extinction coefficient of $0.14 \cdot m^{-1}$.

Outlier Year 1977

Spring TP and Chl *a* concentrations were lowest in 1977 and Secchi depths were deeper. Rockwell et al. (1980b) demonstrated that reduced TP and Chl *a* concentrations in 1977 were evident on a lake-wide scale (see also Fig. 1 and 2a) and were not a regional phenomenon.

Winter and early spring winds, under isothermal or weakly stable conditions, typically resuspend deepwater and recently settled particulate material. Analysis of sedimentation and resuspension fluxes via sediment trap collections in Lake Michigan (Eadie et al. 1984) indicates that this winter and early spring resuspension provides the major upward flux of TP and subsequently resets TP conditions prior to the onset of stratification each year. During the severe winter of 1976–77, extensive ice cover developed, ranging up to 90% coverage

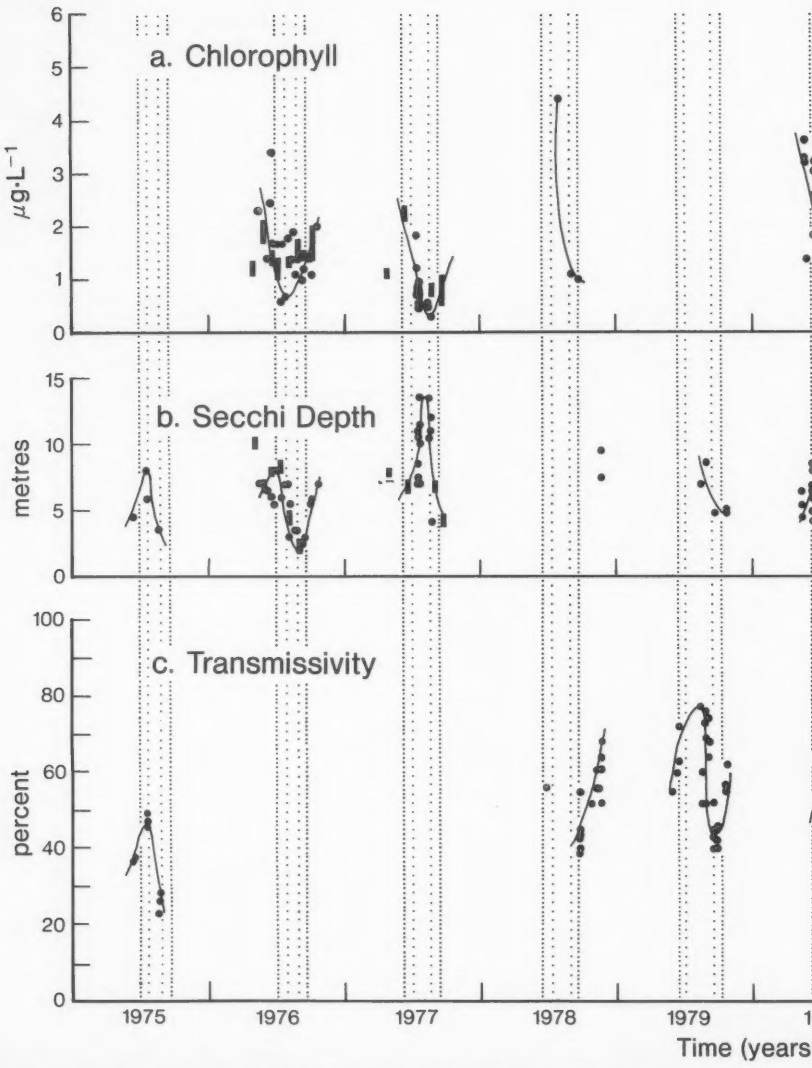
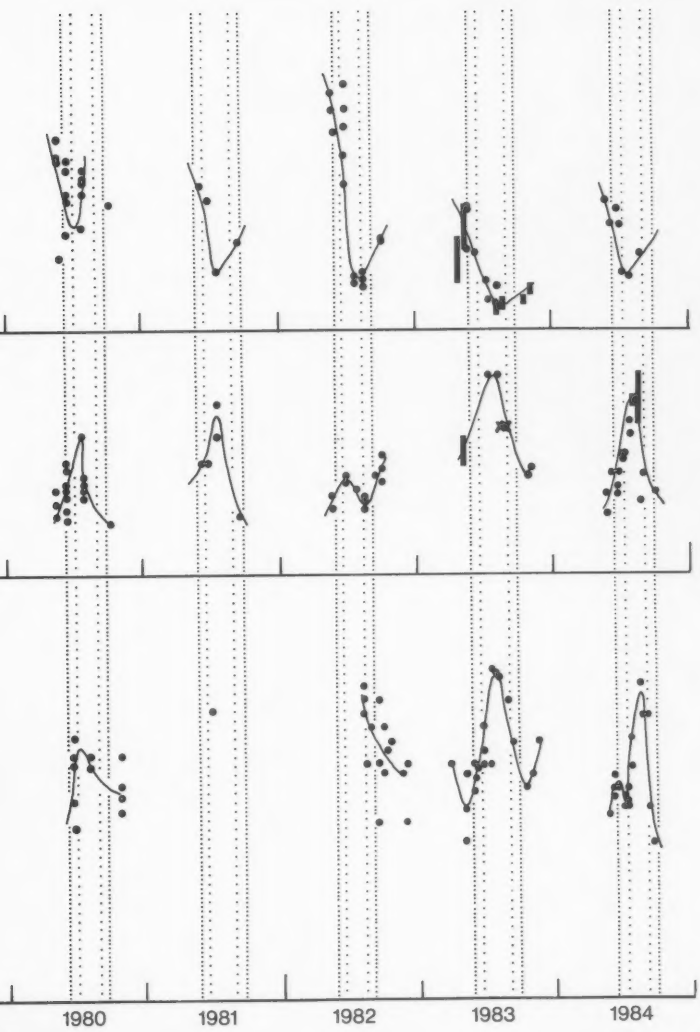


FIG. 2. Chlorophyll *a* and water clarity properties from the southern basin of Lake Michigan for 1975–
greater than 80 m. Other data are from the region off Grand Haven, MI. (a) Epilimnetic chlorophyl
than 11 m; (c) epilimnetic average light transmittance through 1-m path. The width of the stippled b
thermocline deepens past 15 m.



for 1975–84. Vertical bars represent means ±1 SE from southern basin stations with depths
chlorophyll *a*; (b) Secchi disk depth (symbol X represents EPA observations reported as greater
stippled bars marks the period from the onset of stratification through the time when the

TABLE 1. Photosynthetically active radiation (PAR) extinction coefficients (K_e) and depth of 1% surface irradiance.

Date	K_e (m^{-1})	1% light depth (m)
1982		
May 20	0.21	22.0
June 13	0.21	22.0
July 21	0.17	27.0
1983		
May 20	0.18	25.6
June 6	0.19	24.2
June 8	0.17	27.0
July 10	0.14	32.8
July 13	0.14	32.8
1984		
May 21	0.21	22.0
June 4	0.21	22.0
June 18	0.19	24.2
July 25	0.20	23.0
July 30	0.17	27.0
August 24	0.23	20.0

(Quinn et al. 1978). Lake Michigan ice cover typically ranges from 20 to 50% and is restricted mostly to the nearshore area in the southern basin (Assel et al. 1983). Rodgers and Salisbury (1981) reproduced the 1976–77 TP transition in a simulation model by both reducing vertical mixing and increasing the effective sedimentation rate during winter to mimic lower resuspension flux caused by ice cover. While mechanisms relating winter resuspension flux to entrained wind energy and its dissipation by ice are tentative (Lesht and Rockwell 1985), this hydrologic phenomenon may have reduced resuspension, which in turn resulted in lower spring TP concentrations. Approximately 20% of resuspended phosphorus is available for algal production (NaOH extractions (Eadie et al. 1984)). It is not surprising, then, that, as we have shown above, reduced 1977 spring TP concentrations would affect algal production and lead to reduced Chl *a* concentrations (Fig. 2a) and increased water clarity (Fig. 2b) in summer.

Outlier Years 1983–84

Winter 1982–83 was not severe and ice cover was not particularly extensive; spring TP also did not vary substantially from the overall trend; therefore the basis for reduced Chl *a* and increased water clarity in 1983 requires further analysis. In addition to nutrient supply, algal abundance is controlled through zooplankton grazing.

Zooplankton grazing

Examination of the 10-yr record of total zooplankton biomass during the time of the midsummer Chl *a* minimum (Fig. 3a) shows no particular trend and, more specifically, nothing unusual in 1983. The zooplankton of 1983 and 1984 were, however, different from other years in another important way. Prior to 1983, calanoid copepods (primarily *Diaptomus* spp.) dominated the Lake Michigan summer zooplankton, and in those years, *Daphnia* spp. were a relatively minor component (14.1 ± 6.6% by weight). However, *Daphnia* spp. constituted 50–70% and 40–50% of the zooplankton (0–40 m) biomass during July–August 1983 and 1984, respectively. Furthermore, the numerically dominant *Daphnia* was *D. pulicaria*. This species was first observed in southeastern Lake Michigan in autumn 1978 but did not become a summer dominant until 1982 (Evans 1985; Evans and Jude 1986). *Daphnia pulicaria* is a relatively large cladoceran, attaining adult body lengths greater than 2.4 mm and dry weights of 39.8 μg. *Daphnia retrocurva* and *D. galeata mendotae*, the previously dominant cladocerans, are smaller, averaging 2.9 and 4.0 μg dry weight, respectively.

Increased water transparency, independent of changes in nutrient status, has been reported for other lakes and has been associated with increased abundance of *Daphnia* (e.g. Shapiro et al. 1975; Lampert 1978; Edmondson and Litt 1982). We measured the grazing pressure exerted by this *Daphnia*-dominated community in August 1983; this experiment yielded a filtering rate of 7.09 ± 1.0 $mL \cdot \mu g^{-1} \cdot d^{-1}$. (Our estimates are conservative because we included in our analysis injured or dead animals whose injuries may have been sustained during incubation.) With total animal dry weight of 79.0 ± 21.6 $\mu g \cdot L^{-1}$, we calculate that only 1.8 d would be required to clear the epilimnion in August 1983. Comparing this with estimated 3-d turnover times for the algal populations present in August 1983 (G. L. Fahnenstiel and D. Scavia, unpubl. data) indicates the ability of this zooplankton community to clear phytoplankton from the epilimnion.

We also measured grazing pressure in June 1983. Although conditions in June are different from those in midsummer, zooplankton composition in June 1983 was similar to that found in midsummer of previous years (approximately 75–80% by weight as *Cyclops* spp. and *Diaptomus* spp.). These experiments yielded filtering rates of 2.46 ± 0.62 $mL \cdot \mu g^{-1} \cdot d^{-1}$, which, for zooplankton dry weight of 79 $\mu g \cdot L^{-1}$, would yield epilimnion clearance times greater than 5 d in contrast with 1.8 d for the *Daphnia*-dominated assemblage. In June, copepods were predominantly (approximately 75% by weight) *Diaptomus* copepodites. Adults can be more abundant in summer. Filtering rates determined in the laboratory for adult *Diaptomus* spp. feeding during summer in suspensions of Lake Michigan seston range from 0.2 to 0.3 $mL \cdot \mu g^{-1} \cdot d^{-1}$ (Vanderploeg and Scavia 1979; Vanderploeg 1981; H. A. Vanderploeg, GLERL, unpubl. data). These rates yield a turnover time for the total seston of approximately 50 d! *Diaptomus sicilis* and *D. ashlandi* filtering rates, determined for Lake Michigan by measuring changes in only Chl *a* during feeding bouts (Bowers 1980), are similar (0.1 and 0.5 $mL \cdot \mu g^{-1} \cdot d^{-1}$, assuming 17.3 and 4.8 μg dry weight per individual (Hawkins and Evans 1979)) to those determined on the total seston, illustrating the selective nature of feeding by these calanoids. Cladocerans, which are less selective than copepods in terms of both particle size and scent (Richman and Dodson 1983; Muck and Lampert 1984; Vanderploeg and Paffenhöfer 1985), will have an even more pronounced effect on the total seston than on Chl *a* concentration only. It appears that the restructured midsummer zooplankton in 1983 and 1984 was capable of reducing seston concentrations below previous midsummer levels, resulting in increased water clarity.

Causes for zooplankton species changes

If food quality and quantity are major regulators of zooplankton species composition, then several lines of evidence lead to the conclusion that large cladocerans (e.g. *Daphnia* spp.) should dominate the Lake Michigan assemblage. It has been claimed (Richman and Dodson 1983) that cladocerans such as *Daphnia* occupy niches characterized by moderately abundant high-quality food whereas calanoid copepods dominate in areas

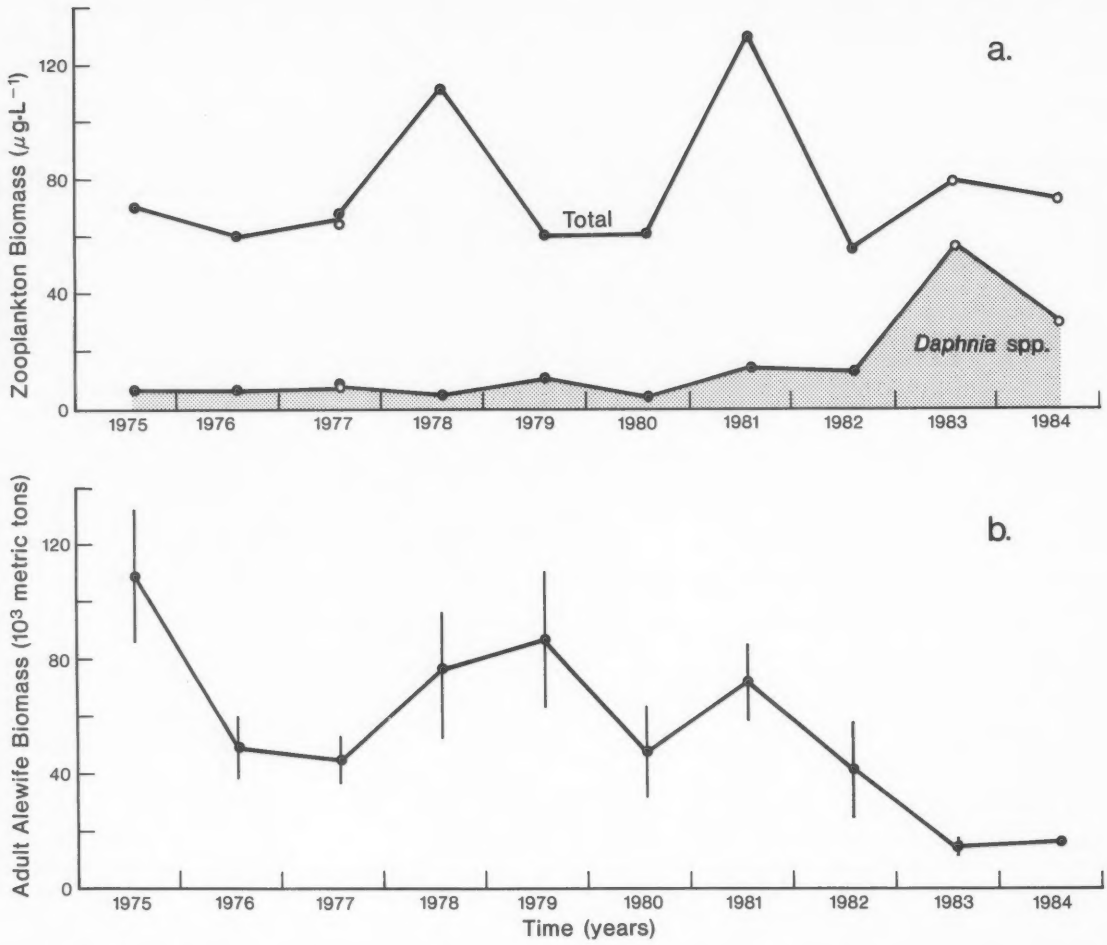


FIG. 3. (a) Dry weight of zooplankton collected during July and August 1975–84. Open points represent data collected from a 100-m station off Grand Haven, MI. Solid points represent data from a 40-m station south of Grand Haven (off Bridgman, MI). (b) Means and SE of estimates of lake-wide averaged adult alewife biomass.

of either lower food quality or lower food abundance. Food quality is a relative measure; however, we suggest that Lake Michigan seston concentration and quality is conducive to a cladoceran advantage. Richman and Dodson (1983) used serial dilutions of southern Green Bay water (mostly species of the algae *Anabaena*, *Aphanizomenon*, *Microcystis*, and *Oscillatoria*) with a mixture of cultured, edible green algae to prepare a gradient of quality for testing the above hypothesis. Vanderploeg et al. (1984) suggested that Lake Michigan seston is of lower quality relative to cultured algae; however, the food quality of open Lake Michigan seston is certainly greater than that of southern Green Bay. In fact, Vanderploeg (1981) explained invariance of measured particle selection by *Diaptomus* by ascribing high quality to the large particles and to at least some small particles of the Lake Michigan seston. Recently, Muck and Lampert (1984) further quantified the competitive regimes of the copepod *Eudiaptomus* and *Daphnia*. At low food concentrations, these two species had very similar weight-specific ingestion rates. Because the calanoid copepod expends less energy at low food concentrations, it should outcompete *Daphnia*. However, the copepod ingestion rate saturates at a lower value and at a lower food concentration than that of *Daphnia*. Thus, at higher food concentrations, *Daphnia* should be superior. The incipient limiting level, when ingestion rate saturates for *Eudiaptomus*, is approximately 100 $\mu g\ C \cdot L^{-1}$. A similar level for *Diaptomus sicilis* is apparent from fig. 3 and 10 of Vanderploeg et al. (1984). Particulate organic carbon concentrations in this region of Lake Michigan are typically 200 $\mu g\ C \cdot L^{-1}$ (Eadie et al. 1984), and even if that value is halved to estimate an "effective food concentration" (Vanderploeg and Scavia 1979; Vanderploeg et al. 1984), it appears that food levels are at or above the limiting level for the copepods. If the above hypothesis is correct, then, based on both food quantity and quality, *Daphnia*-like cladocerans should have been abundant in this region of Lake Michigan if resource-based competition is the dominant force shaping the assemblage. They were not.

We suggest that predatory pressure from the planktivorous

alewife suppressed large-bodied zooplankton populations until the early 1980s, when the alewife population decreased to new low levels (Fig. 3b). Alewife, an exotic marine species that invaded the upper Great Lakes through the Welland Canal (Smith 1968, 1970), was first reported in Lake Michigan during the late 1940s (Miller 1957) and has dominated the Lake Michigan fish planktivore population for the past 20 yr. Its population dynamics have been well documented (Brown 1972; Hatch et al. 1981; Jude and Tesar 1985; Eck and Brown 1985), and its impact on Lake Michigan zooplankton is consistent with size-selective predation theories (Hrbáček 1962; Dodson 1974). During periods of great alewife abundance (e.g. 1966), large zooplankton (1.1−5.0 mm) that were previously abundant became rare (Wells 1970). During a massive alewife die-off in 1966−67 (Brown 1972), these large zooplankton increased in abundance.

In the early 1980s alewife abundances again declined (Jude and Tesar 1985), and in 1983 and 1984 they decreased dramatically to their lowest levels since the early 1960s (Wells and Hatch 1984; L. Wells, pers. comm.). This dramatic decrease in alewife abundance has again relieved the larger zooplankton from strong vertebrate predation. Furthermore, a new species, *D. pulicaria*, became the new dominant replacing the smaller *Daphnia* that were most abundant in years before alewife invaded. *Daphnia pulicaria* become reproductive at a body length of 1.6 mm (Edmondson and Litt 1982), and intense size-selective predation pressure from alewife prior to 1982 probably prevented population growth even though the species was observed as early as autumn 1978 in the nearshore region (Evans et al. 1980; Evans and Jude 1986).

Alewife decline

Decline of the alewife population as the major forage fish in Lake Michigan was predicted (Smith 1970; Christie 1974; Stewart et al. 1981) and has been linked to management actions involving salmonid stocking. Because the number of stocked salmonines is not linked functionally to their forage base, Stewart et al. (1981) estimated that salmonines would place a demand on prey resources that might outstrip the alewife's reproductive capacity. An alternative view attributes the alewife decline to changes in the physical environment (a series of cold winters) rather than current levels of salmonine predation (Eck and Brown 1985). Salmonine predation, in that case, exerts additional pressure on the alewife population.

The following hypothesis provides the senario for "outlier" year 1983 and beyond. An aggressive salmonine stocking program (Stewart et al. 1981; Jude and Tesar 1985) and several recent cold winters (Eck and Brown 1985) have contributed to dramatic decreases in the abundance of alewife, the major open-water planktivore. This decrease in vertebrate planktivory allowed *Daphnia* spp. to dominate the summer zooplankton and, because of their higher filtering capacities and less selective feeding, reduce Chl *a* and probably total seston concentrations. This resulted in increased water clarity[2].

It is not known whether 1983 is an "outlier" year or the beginning of a new sequence of years reflecting a dramatic reduction in the alewife population and its effect on zooplankton. In either case, it seems reasonable to hypothesize that, for Lake Michigan, management actions at the top of the ecosystem have cascaded (Carpenter and Kitchell 1984; Carpenter et al. 1985; Kitchell and Carpenter 1986) to effects on properties at several lower trophic levels, even to water clarity.[2]

General Discussion

We have shown both long-term, gradual changes in TP and water clarity and two periods of deviation from the long-term trend. The long-term data are consistent with expectations of nutrient load control. These gradual changes in TP and barely perceptible changes in Chl *a* are expected (Vollenweider et al. 1980) from consideration of the long hydraulic residence time (Chapra and Sonzogni 1979) and realized nutrient load reductions (International Joint Commission 1984). The observations reported here for the region offshore of Grand Haven are similar to southern basin averages of TP and Chl *a* in 1976, 1977, 1983, and 1984 (see Fig. 1 and 2 and Lesht and Rockwell 1985). These results suggest that, in terms of TP, the management objective of "nondegradation" has been accomplished because concentrations have decreased by about 30% since 1976. Summer Chl *a* concentrations have not decreased in a similar gradual fashion. In fact, little change in the midsummer, clear phase minimum has been seen except for "outlier" years. However, gradual improvement has been observed in measures of summer water clarity, which are indirect and, at low Chl *a* concentrations, amplified manifestations of Chl *a* changes (Chapra and Dobson 1981). While the gradual trend toward lower TP and clearer water is consistent with the objectives and actions of the phosphorus load reduction program, the latter has not been proven to be the causal mechanism. It would be useful to examine alternative hypotheses (e.g. Brooks et al. 1984). The influence of physical factors on the Great Lakes ecosystems has been recognized for a long time (e.g. Chandler and Weeks 1945) and reiterated recently (Harris and Vollenweider 1982). Analysis of "outlier" year 1977 illustrates the effects that dramatic meteorological events can have on an aquatic ecosystem, even for a lake as large as Lake Michigan. Interestingly, the drop in TP and the lower Chl *a* minimum in 1977 lasted only 1 yr, after which both properties became consistent with long-term trends. Eck and Brown (1985) reported that winters near Lake Michigan have been colder than the 1949−83 mean for all but one of the years between 1976 and 1983. Comparison of the TP trend with the potentially subtle variations in ice cover or winter severity over the past decade would test the hypothesis that winter physics also exerts control over spring TP. It is clear from our analysis that many environmental factors must be considered when evaluating long-term water quality trends.

Results from 1983 and 1984 demonstrate that forces acting at the very top of the Lake Michigan food web may drive the ecosystem in a new direction. The impact of planktivore population dynamics on the zooplankton of this lake has been demonstrated before (Wells 1970; Kitchell and Carpenter 1986), but we now hypothesize that forces at the top of the food web have caused changes in the base, in a clearer water column, and thus have modified one of the most important parameters of perceived water quality.

Stability of this condition is currently uncertain. Data from 1984 suggest that, while alewife populations are still at very low levels, other planktivores (particularly bloater, *Coregonus*

[2]FOOTNOTE ADDED IN PRESS: Conditions in the region off Grand Haven, observed in 1983 and 1984, continued to persist in 1985. Summer Secchi depths were deeper than 14 m, epilimnetic Chl *a* concentrations were as low as 0.5 $\mu g \cdot L^{-1}$, and epilimnetic transmissivity remained very high in 1985. Alewife biomass remained low and *Daphnia* was again abundant during summer.

hoyi, and yellow perch, *Perca flavescens*) are still increasing in abundance (L. Wells, pers. comm.). The impact of the alewife decline on invertebrate predators is also unclear at this time; however, one would expect an increase in abundance of the large invertebrates (e.g., *Mysis relicta*, *Limnocalanus macrurus*) that coincide spatially and temporally with the alewife. The impact of these invertebrate predators on other zooplankton may also influence species composition (Lynch 1979), and these predators may also have been responsible for the somewhat reduced relative abundance of *Daphnia* spp. in 1984 (Fig. 3a) and the continued changes in *Daphnia* spp. size and composition in 1984.

Salmonine stocking programs continue to grow in other of the Great Lakes. Given the dramatic changes observed in Lake Michigan in the recent past, we can expect similar response potential in the food webs of other systems. We should take advantage of those opportunities for gaining greater understanding of the mechanisms that control water quality in systems where management activities influence the processes associated with both nutrient loading and food web regulation of nutrient cycles. Weather-related effects remain stochastic and largely uncontrollable, but the prospects for improvement of water quality through food web management remain open to development and testing. Only by continuing evaluation of the dynamics of Lake Michigan and the other Great Lakes during this period of transition will we be able to assess the relative impact of our actions in light of natural variability.

Acknowledgments

Several individuals graciously provided access to unpublished data. We thank G. A. Bell, B. J. Eadie, W. S. Gardner, N. Hawley, J. M. Malcyzk, S. J. Tarapchak, and H. A. Vanderploeg of the Great Lakes Environmental Research Laboratory (NOAA), J. A. Bowers and R. A. Moll of the Great Lakes Research Division (University of Michigan), L. Wells of the Great Lakes Fishery Laboratory (U.S. Fish and Wildlife Service), B. M. Lesht of Argonne National Laboratory, and D. C. Rockwell of the Great Lakes National Program Office (U.S. Environmental Protection Agency) for those data. We also appreciate the improvements to the manuscript suggested by W. S. Gardner, J. F. Kitchell, A. Robertson, H. A. Vanderploeg, and an anonymous reviewer. Some of the zooplankton collections were supported by the Indiana and Michigan Electric Company and Michigan Sea Grant, grants to M. S. Evans, and by NSF grant DEB81-16428 to J. T. Lehman.

References

ASSEL, R. A., F. H. QUINN, G. A. LESHKEVICH, AND S. J. BOLSENGA. 1983. NOAA Great Lakes Ice Atlas. Great Lakes Environmental Research Laboratory. Ann Arbor, MI. 120 p.

BARTONE, C. R., AND C. L. SCHELSKE. 1982. Lake-wide seasonal changes in limnological conditions in Lake Michigan, 1976. J. Great Lakes Res. 8: 413–427.

BOWERS, J. A. 1980. Feeding habits of *Diaptomus ashlandi* and *Diaptomus sicilis* in Lake Michigan. Int. Rev. Gesamten Hydrobiol. 65: 259–267.

BOYCE, F. M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. J. Fish Res. Board Can. 31: 689–730.

BROOKS, A. S., AND B. G. TORKE. 1977. Vertical and seasonal distribution of chlorophyll *a* in Lake Michigan. J. Fish. Res. Board Can. 34: 2280–2287.

BROOKS, A. S., G. J. WARREN, M. E. BORAAS, D. B. SEALE, AND D. N. EDGINGTON. 1984. Long-term phytoplankton changes in Lake Michigan: cultural eutrophication or biotic shifts. Verh. Int. Ver. Limnol. 22: 452–459.

BROWN, E. H. JR. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949–70. J. Fish. Res. Board Can. 29: 477–500.

CARPENTER, S. R., AND J. F. KITCHELL. 1984. Plankton community structure and limnetic primary production. Am. Nat. 124: 159–172.

CARPENTER, S. R., J. F. KITCHELL, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake ecosystem productivity. Bioscience 35: 634–639.

CHANDLER, D. C., AND O. B. WEEKS. 1945. Limnological studies of western Lake Erie. V. Relation of limnological and meteorological conditions to the production of phytoplankton in 1942. Ecol. Monogr. 15: 436–457.

CHAPRA, S. C., AND H. F. H. DOBSON. 1981. Quantification of the lake trophic typologies of Naumann (surface quality) and Thienemann (oxygen) with special reference to the Great Lakes. J. Great Lakes Res. 7: 182–193.

CHAPRA, S. C., AND W. C. SONZOGNI. 1979. Great Lakes total phosphorus budget for the mid 1970s. J. Water Pollut. Control Fed. 51: 2524–2533.

CHRISTIE, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

DENMAN, K. L., AND T. M. POWELL. 1984. Effects of physical processes on planktonic ecosystems in the Coastal Ocean. Oceanogr. Mar. Biol. Annu. Rev. 22: 125–168.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–774.

DOBSON, H. F. H. 1981. Trophic conditions and trends in the Laurentian Great Lakes. W. H. O. Water Qual. Bull. 6: 146–151, 158, 160.

DODSON, S. E. 1974. Adaptative change in plankton morphology in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721–729.

EADIE, B. J., R. L. CHAMBERS, W. S. GARDNER, AND G. L. BELL. 1984. Sediment trap studies in Lake Michigan: resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. 10: 307–321.

ECK, G. W., AND E. H. BROWN, JR. 1985. Lake Michigan's capacity to support lake trout and other salmonines: an estimate based on the status of prey populations in the 1970s. Can. J. Fish. Aquat. Sci. 42: 449–454.

EDMONDSON, W. T., AND A. H. LITT. 1982. *Daphnia* in Lake Washington. Limnol. Oceanogr. 27: 272–293.

ESHENRODER, R. L., T. P. POE, AND C. H. OLVER [ED.] 1984. Strategies for rehabilitation of lake trout in the Great Lakes. Proceedings of a conference on lake trout research, August 1983. Great Lakes Fishery Commission, Ann Arbor, MI.

EVANS, M. S. 1985. The morphology of *Daphnia pulicaria*, a species newly dominating the southeastern Lake Michigan summer *Daphnia* community. Trans. Am. Microsc. Soc. 104: 223–231.

EVANS, M. S., B. E. HAWKINS, AND D. W. SELL. 1980. Seasonal features of zooplankton assemblages in the nearshore area of southeastern Lake Michigan. J. Great Lakes Res. 6: 275–289.

EVANS, M. S., AND D. J. JUDE. 1986. Recent shifts in *Daphnia* community structure in southeastern Lake Michigan: a comparison of the inshore and offshore regions. Limnol. Oceanogr. 31: 56–67.

HARRIS, G. P., AND R. A. VOLLENWEIDER. 1982. Paleolimnological evidence of early eutrophication in Lake Erie. Can. J. Fish. Aquat. Sci. 39: 618–626.

HATCH, R. W., P. M. HAACK, AND E. H. BROWN, JR. 1981. Estimation of alewife biomass in Lake Michigan, 1967–1978. Trans. Am. Fish. Soc. 110: 575–584.

HAWKINS, B. E., AND M. S. EVANS. 1979. Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. J. Great Lakes Res. 5: 256–263.

HRBÁČEK, J. 1962. Species composition and the amount of zooplankton in relation to the fish stocks. Rozpr. Cesk. Akad. Ved. 72: 1–116.

INTERNATIONAL JOINT COMMISSION. 1984. 1983 Report of the Great Lakes Water Quality Board to the International Joint Commission. Appendix — Great Lakes Surveillance. International Joint Commission, Windsor, Ont. 129 p.

JUDE, D. J., AND F. J. TESAR. 1985. Recent changes in the forage fish of Lake Michigan. Can. J. Fish. Aquat. Sci. 42: 1154–1157.

KITCHELL, J. F., AND S. R. CARPENTER. 1986. Piscivores, planktivores, fossils, and phorbins. *In* W. C. Kerfoot [ed.] Predation: effects on aquatic communities. University Press of New England, Hanover, NH. (In press)

LADEWSKI, T. B., AND E. F. STOERMER. 1973. Water transparency in southern Lake Michigan in 1971 and 1977. Proc. Conf. Great Lakes Res. 16: 791–807.

LAMPERT, W. 1978. Climatic connections and planktonic interactions as factors controlling the regular succession of spring algal bloom and extremely clear water in Lake Constance. Verh. Int. Ver. Limnol. 20: 969.

LEHMAN, J. T. 1980. Release and cycling of nutrients between planktonic algae and herbivores. Limnol. Oceanogr. 25: 620–632.

LESHT, B. M., AND D. C. ROCKWELL. 1985. The status of the middle Great Lakes: results of the 1983 water quality survey of Lakes Erie, Huron, and Michigan. Rep. No. ANL/ER-85-2, Argonne National Laboratory, Argonne, IL. 118 p.

LYNCH, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. Limnol. Oceanogr. 24: 253–272.

MCQUEEN, D. J., S. S. RAO, AND D. R. S. LEAN. 1984. Hypolimnetic aeration changes in bacterial populations and oxygen demand. Arch. Hydrobiol. 90: 498–514.

MILLER, R. R. 1957. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. Trans. Am. Fish. Soc. 86: 97–111.

MUCK, P., AND W. LAMPERT. 1984. An experimental study on the importance of food conditions for the relative abundance of calanoid copepods and cladocerans. 1. Comparative feeding studies with *Eudiaptomus gracilis* and *Daphnia longispina*. Arch. Hydrobiol. Suppl. 66: 157–179.

PARKER, J. I., H. L. CONWAY, AND E. M. YAGUCHI. 1977. Seasonal periodicity of diatoms and silicon limitation in offshore Lake Michigan, 1975. J. Fish. Res. Board Can. 34: 552–558.

QUINN, F. H., R. A. ASSEL, D. E. BOYCE, G. A. LESHKEVICH, C. R. SNIDER, AND D. WEISNET. 1978. Summary of Great Lakes weather and ice conditions, winter 1976–77. NOAA Tech. Mem. ERL GLERL-20.

RICHMAN, S., AND S. I. DODSON. 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. Limnol. Oceanogr. 28: 948–956.

ROCKWELL, D. C., D. S. DEVAULT, M. F. PALMER, C. V. MARION, AND R. J. BOWDEN. 1980a. Lake Michigan Intensive Survey 1976–1977. U.S. Environmental Protection Agency, EPA-905/4-80-003-A. Great Lakes National Program Office, Chicago, IL. 154 p.

ROCKWELL, D. C., C. V. MARION, M. F. PALMER, D. S. DEVAULT, AND R. J. BOWDEN. 1980b. Environmental trends in Lake Michigan, p. 91–132. *In* R. C. Loehr, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

RODGERS, P., AND D. SALISBURY. 1981. Water quality modeling of Lake Michigan and consideration of the anomalous ice cover of 1976–1977. J. Great Lakes Res. 7: 467–480.

SCHELSKE, C. L. 1979. Role of phosphorus in Great Lakes eutrophication. Is there a controversy? J. Fish. Res. Board Can. 36: 286–288.

SHAPIRO, J., V. A. LAMARRA, AND M. LYNCH. 1975. Biomanipulation: an ecosystem approach to lake restoration, p. 85–96. *In* P. L. Brezonik and J. L. Fox [ed.] Proceedings of the Symposium on Water Quality Management Through Biological Control. University of Florida and USEPA, Gainesville, FL, Jan. 29–31.

SHAPIRO, J., AND D. J. WRIGHT. 1983. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwater Biol. 14: 371–384.

SLATER, R. W., AND G. E. BANGAY. 1980. Action taken to control phosphorus in the Great Lakes, p. 13–26. *In* R. C. Loehr, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

SMITH, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99: 754–765.

SOMMER, U. 1984. The periodicity of phytoplankton in Lake Constance in comparison to other deep lakes of Central Europe. Verh. Int. Ver. Limnol. 22: 963. (Abstr.)

SONZOGNI, W. S., A. ROBERTSON, AND A. M. BEETON. 1983. Great Lakes management: ecological factors. Environ. Manage. 7: 531–542.

SPIGEL, R. H., AND C. HOWARD-WILLIAM. 1984. A method for comparing scalar irradiance measurements with upward and downward irradiance in lakes. Water Resour. Res. 20: 507–509.

STENSON, J. A. E., T. BUHEIN, L. HENRICKSON, B. I. NILSSON, H. B. NYMAN, H. G. OSCARSON, AND P. LARSSON. 1978. Effects of fish removal from a small lake. Verh. Int. Ver. Limnol. 20: 794–801.

STEWART, D. J., J. F. KITCHELL, AND L. B. CROWDER. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

STRONG, A. E., AND B. J. EADIE. 1978. Satellite observation of calcium carbonate precipitations in the Great Lakes. Limnol. Oceanogr. 23: 877–887.

VANDERPLOEG, H. A. 1981. Seasonal particle-size selection by *Diaptomus sicilis* in offshore Lake Michigan. Can. J. Fish. Aquat. Sci. 38: 504–517.

VANDERPLOEG, H. A., AND G.-A. PAFFENHÖFER. 1985. Modes of algal capture by the freshwater copepod *Diaptomus sicilis* and their relation to food-size selection. Limnol. Oceanogr. 30: 871–885.

VANDERPLOEG, H. A., AND D. SCAVIA. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol. Model. 7: 135–149.

VANDERPLOEG, H. A., D. SCAVIA, AND J. P. LIEBIG. 1984. Feeding rate of *Diaptomus sicilis* and its relation to selectivity and effective food concentration in algal mixtures and in Lake Michigan. J. Plankton Res. 6: 919–941.

VOLLENWEIDER, R. A., W. RAST, AND J. KEREKES. 1980. The phosphorus loading concept and Great Lakes eutrophication, p. 207–234. *In* R. C. Loehr, C. S. Martin, and W. Rast [ed.] Phosphorus management strategies for lakes. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

WALTERS, C. J., G. SPANGLER, W. J. CHRISTIE, P. J. MANION, AND J. F. KITCHELL. 1980. A synthesis of knowns unknowns, and policy recommendations from the Sea Lamprey International Symposium. Can. J. Fish. Aquat. Sci. 37: 2202–2208.

WELLS, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

WELLS, L., AND R. W. HATCH. 1984. Status of bloater chubs, alewives, smelt, slimy sculpins, deepwater sculpins, and yellow perch in Lake Michigan, 1984, p. 29–36. *In* Appendices to Lake Michigan Committee 1984 annual meeting minutes. Great Lakes Fishery Commission, Ann Arbor, MI.

Limnetic Zooplankton Assemblages in Atlantic Canada with Special Reference to Acidification

J. C. H. Carter and W. D. Taylor

Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1

R. Chengalath

Invertebrate Zoology Division, National Museum of Natural Sciences, Ottawa, Ont. K1A 0M8

and D. A. Scruton

Department of Fisheries and Oceans, Fisheries Research Branch, P.O. Box 5667 St. John's, Nfld. A1C 5X1

Carter, J. C. H., W. D. Taylor, R. Chengalath, and D. A. Scruton. 1986. Limnetic zooplankton assemblages in Atlantic Canada with special reference to acidification. Can. J. Fish. Aquat. Sci. 43: 444–456.

Crustacean and rotifer plankton assemblages of 93 lakes in Labrador, 107 in Newfoundland, and 142 in New Brunswick – Nova Scotia were investigated for evidence of correlations with lake morphometric, chemical, or biological factors. Labrador assemblages were almost completely lacking in identifiable structure. Newfoundland species clustered into two groups of different body size, suggesting the influence of fish predation. Only one species in Labrador and Newfoundland was significantly correlated with a derived factor related to lake water buffering capacity. New Brunswick – Nova Scotia species clustered into two groups, one featuring significant positive and the other significant negative correlations with the buffering factor. From this we conclude that acidification is having an impact on the limnetic zooplankton of these two provinces. Multiple discriminant analysis was used to demonstrate that New Brunswick – Nova Scotia lakes differing in their buffering capacity were also distinct in zooplankton composition. Lakes with low factor scores (low pH, alkalinity, and calcium) were mainly located in the Bay of Fundy region; this area has above average fog and precipitation, and lies within the summer air flow carrying pollutants from the south.

Des groupes de crustacés et de rotifères planctoniques de 93 lacs du Labrador, de 107 de Terre-Neuve et de 142 du Nouveau-Brunswick et de la Nouvelle-Écosse ont été étudiés pour la recherche de corrélations avec des facteurs ayant trait à la morphométrie, à la chimie ou à la biologie des lacs. Les groupes du Labrador ne présentaient pratiquement aucune structure identifiable. Les espèces de Terre-Neuve se divisaient en deux groupes de taille différente, ce qui porte à croire à une influence de la prédation par les poissons. Une seule espèce du Labrador et de Terre-Neuve présentait une corrélation significative avec un facteur secondaire lié au pouvoir tampon des eaux du lac. Les espèces du Nouveau-Brunswick et de la Nouvelle-Écosse se divisaient en deux groupes présentant respectivement une corrélation significativement positive ou significativement négative avec le pouvoir tampon. Les auteurs concluent à un effet de l'acidification sur le zooplancton limnétique de ces deux provinces. Une analyse par discriminants multiples a permis de montrer que les lacs du Nouveau-Brunswick et de la Nouvelle-Écosse qui différaient de par leur pouvoir tampon différaient aussi de par leur composition zooplanctonique. Les lacs à facteur de qualité moindre (pH, alcalinité et teneur en calcium peu élevés) se retrouvaient surtout dans la région de la baie de Fundy; cette région, à brouillards et précipitations supérieurs à la moyenne, est située dans l'axe des vents d'été apportant des polluants en provenance du sud.

Received May 14, 1985
Accepted October 21, 1985
(J8239)

Reçu le 14 mai 1985
Accepté le 21 octobre 1985

Species composition and abundance of limnetic zooplankton generally reflect the influence of one or more environmental variables. The most frequently cited biotic variable is predation. Planktivorous fish and predaceous invertebrates may radically alter zooplankton assemblages by reducing or eliminating large and small prey species, respectively (Zaret 1980). Lake morphometry may also be important (Patalas 1971) although whether community structure is affected by morphometric variables per se, or rather by associated trophic factors, is often unclear.

Because the negative effects of acidification have become increasingly manifest, attention has focused on water chemistry, especially pH and its correlates, as a major regulator of aquatic ecosystems. Studies in Europe (e.g. Almer et al. 1974; Fryer 1980) and North America (e.g. Yan and Strus 1980; Keller and Pitblado 1984; Brezonik et al. 1984) have demonstrated clear differences in zooplankton communities between acidic and nonacidic lakes. Unfortunately, few, if any, investigations include zooplankton data from earlier, preacidification periods, and consequently, community changes over time must be inferred by contrast with nonacidified lakes within the same area.

Despite the geological sensitivity of most of Labrador and much of Newfoundland, acidification of lakes has been docu-

TABLE 1. Factor analysis of lake variables: correlation coefficients between derived factors and original chemical and morphometric variables in each of the three regions. A dash indicates that the variable was not measured. Coefficients <0.250 are replaced by zero. TDS = total dissolved solids; DA = drainage basin area; LSA = lake surface area; DOC = dissolved organic carbon.

	Labrador				Newfoundland					New Brunswick – Nova Scotia			
	1	2	3	4	1	2	3	4	5	1	2	3	4
pH	0.83	−0.34	0	0	0.91	0	0	0	0	0.80	0	0	0
Alkalinity	0.91	0	0	0	0.95	0	0	0	0	0.87	0	0	0
Calcium	0.93	0	0	0	0.90	0.28	0	0	0	0.92	0	0	0
Magnesium	0.92	0	0	0	0.72	0.57	0	0	0	0.66	0.62	0	0
Sodium	0.43	0	0	0.73	0.27	0.89	0	0	0	0	0.95	0	0
Potassium	0.49	0.28	0.26	−0.33	0.45	0.50	0	0	0	0.28	0	0	0.81
Bicarbonate	0.93	0	0	0	0.94	0	0	0	0	—	—	—	—
Chloride	0	0.41	0	0.66	0	0.94	0	0	0	−0.29	0.93	0	0
Sulphate	0.36	0.82	0	0	0	0.60	0.31	0	−0.45	0	0	0	0
Aluminum	−0.33	0.60	0	0.36	−0.26	0.42	0.61	0	0	−0.55	0.29	0.61	0
Iron	—	—	—	—	0	0	0.51	−0.59	0	−0.29	0	0.82	0
Manganese	—	—	—	—	0	0.50	0.36	−0.41	0	0	0	0	0
TDS	0.33	0.71	0	0	0.69	0.63	0	0	0	—	—	—	—
Nitrate	0	0	0	0	−0.29	0	0	0.71	0	—	—	—	—
Turbidity	0	0.72	0	0	0	0.30	0	−0.72	0	—	—	—	—
DOC	0	0.92	0	0	—	—	—	—	—	0	0	0.94	0
Colour	0	0.90	0	0	0	0.28	0.68	−0.39	0	—	—	—	—
Max. depth	0	−0.51	0.67	0	0	0	0	0.75	0	0	0	−0.55	0.65
Mean depth	0	−0.31	0.87	0	—	—	—	—	—	—	—	—	—
LSA	0	0	0.87	0	0	0	−0.30	0	0	—	—	—	—
DA	0	0	0.87	0	0	0	0	0	0.94	—	—	—	—
Ratio (DA:LSA)	0	0	0	0.74	0	0	0.88	0	0.91	—	—	—	—
% variance	24.1	23.0	14.3	9.4	24.2	18.2	11.3	9.9	5.4	25.0	18.6	17.9	9.0

mented for only a small area of Newfoundland (Scruton 1983). However, recent studies in New Brunswick and Nova Scotia indicate that there the process is more advanced (Watt et al. 1979; Wiltshire and Machell 1980; Kerekes et al. 1982).

As part of an extensive monitoring program conducted by the Department of Fisheries and Oceans (DFO) in geologically sensitive areas in eastern Canada, biological, morphometric, and chemical data were collected from 93 headwater lakes in Labrador, 107 in Newfoundland, and 142 in New Brunswick – Nova Scotia. In this report we present the findings of a detailed analysis undertaken to answer the following questions: (1) Is the zooplankton fauna within each of these three major areas composed of distinct species groups? (2) If so, do these groups suggest the influence of any biological, morphometric, or chemical factor. (3) Are species richness and population density related to the morphometric and chemical variables? (4) Is there any evidence of the impact of acidification upon the zooplankton assemblages in any of the three areas?

Methods

In Newfoundland and New Brunswick – Nova Scotia, the lakes were almost all headwater lakes and located in geotypes highly sensitive to potential acidification. Newfoundland lakes ranged in size from 21 to 2500 ha, with a mean of 153 ha; New Brunswick – Nova Scotia lake areas were not calculated. In Labrador, headwater lakes and lakes in highly sensitive geotypes comprised only about 50 and 70%, respectively, of the sample; they ranged in area from 5 to 1215 ha with a mean of 165 ha. Complete details regarding the Newfoundland and Labrador sampling programs are given in Scruton (1983, 1984). No comparable report on the New Brunswick – Nova Scotia survey has been issued.

The numbers of abiotic variables measured were not the same among the three regions, and we used less than the numbers measured. Some we rejected at the outset as irrelevant to the study (e.g. surface temperature on the date of the sample, sediment pH). We also later excluded all the derived chemical variables (e.g. excess sulphate, excess calcium) after concluding from our initial analyses that they were of no assistance in interpreting the zooplankton data. The final list of 22 variables, measured in one or more of the regions, is given in Table 1.

Each lake was sampled on only one occasion as follows: Newfoundland, mid-August to mid-October 1981; Labrador, mid-August to mid-October 1982; New Brunswick – Nova Scotia, July and August, 1981 and 1982. Although Newfoundland and Labrador were sampled later than the two southern provinces, this was not considered a serious drawback because the summer zooplankton should still mainly be present in October, and in any case, the three regions were always kept separate in the analyses.

Field sampling methods were based on techniques set out by the DFO Acid Rain Scientific Committee. However, occasionally, different procedures were used between regions. In Labrador, depths were sounded along transects with a Raytheon DE-719B depth sounder which allowed mean depths to be calculated. In Newfoundland and New Brunswick – Nova Scotia, soundings were made with a lead and line and hence, approximate maximum depths only were obtained. Samples for water analysis in all regions were made with a weighted length of tygon tubing, lowered to the bottom in shallow lakes and to the base of the thermocline in deeper ones. Field pH determinations in Newfoundland and Labrador were

made with a Fisher Accumet 119 portable pH meter and in New Brunswick – Nova Scotia with a Canlab H5503-1 portable pH meter.

Methods for water chemistry analysis were similar among regions. Alkalinities were determined within 24 h using the methods described by the Ontario Ministry of the Environment (1979) and the Ontario Ministry of Natural Resources (1980). All other chemical analyses were performed according to methods described by the American Public Health Association et al. (1975) and Environment Canada (1979). Lake surface areas and drainage basin areas (Newfoundland and Labrador) were determined from aerial photographs and topographic maps, respectively.

Zooplankton was collected with a single vertical haul using a Wisconsin-type plankton net with 20.5-cm mouth diameter, No. 25 mesh (apertures 64 μm), and overall length of 1.2 m. Where the depth was ≥2 m, the haul was made from 1 m above the bottom to the surface; with depths <2 m, a diagonal tow of approximately 1 m was made. Samples were preserved in buffered formalin. All zooplankton was quantified as numbers of individuals per square metre.

Preliminary examination of the data indicated that logarithmic transformation was required for all variables except pH. Factor analysis was used to produce a smaller number of derived variables which were linear combinations of the original chemical and morphological variables. Varimax rotation was used to simplify factor structure. Several cluster analyses were tried, but the UPGMA method (Legendre and Legendre 1983) was selected, as it produced the highest cophenetic correlation coefficients.

Statistical analyses were performed using packages available, at University of Guelph (SAS) and University of Waterloo (SPSS, NTSYS).

Results and Discussion

Environmental Variables and Factor Analysis

Of the 22 chemical and morphometric variables measured we chose 6 that we believed to be most relevant (pH, alkalinity, calcium, maximum depth, sodium, and aluminum) to illustrate differences between lakes of each region. Nova Scotia lakes, with a pH range of 4.0–6.6 and a median of 5.25, were distinctly more acidic than those of the other three regions, where the ranges and median values were very similar (Fig. 1). Nova Scotia lakes also showed a range and median in alkalinity considerably lower than those in other regions. The median for Newfoundland, 1.8 $mg \cdot L^{-1}$, was slightly lower than those for New Brunswick and Labrador. Median calcium ion was low in all regions, despite the presence of a few lakes of moderate calcium hardness, particularly in Newfoundland. The similarity of median values for Nova Scotia and Newfoundland, 0.73 and 0.74 $mg \cdot L^{-1}$, respectively, suggests that the original buffering capacity of most of the lakes in these regions was much the same and only marginally less than that of most Labrador lakes. Median maximum depth was least in Nova Scotia, with New Brunswick lakes only slightly shallower than those in Newfoundland. Labrador, with a number of relatively deep lakes, had both the greatest range of maximum depths and the highest median value. Sodium ion in lake water is usually inversely related to distance from the ocean. Nova Scotia lakes, none farther inland than about 50 km, and the majority much closer, had the highest median sodium content; Labrador, with many lakes remote from the coast, had the lowest. Aluminum ion, which an increasing weight of evidence suggests is toxic to organisms (e.g. Haines 1981) and which enters solution at low pH, had greater ranges and somewhat higher medians in Nova Scotia and Newfoundland. No lake in the entire set contained more than 0.43 mg aluminum $\cdot L^{-1}$ and the great majority had less than 0.2.

Factor analysis was used to reduce the chemical and morphometric data in each of the three areas. Only the first four factors from Labrador and New Brunswick – Nova Scotia, and the first five from Newfoundland, were compound. The remainder comprised single variables with which no species were significantly correlated, and they were therefore dropped from further analysis. In all regions, variables related to the buffering capacity of the water comprised factor 1 and in each case accounted for about 25% of the standardized variance (Table 1). Factor 1 was highly correlated with pH, alkalinity, calcium, and magnesium and, except in New Brunswick – Nova Scotia where no determinations were made, bicarbonate. Aluminum showed low negative correlations with this factor in Labrador and Newfoundland, and a strong negative correlation (−0.55) in New Brunswick – Nova Scotia. Factor 2 in Newfoundland and New Brunswick – Nova Scotia was strongly correlated with sodium and chloride, and was obviously related to marine influence. In Labrador this influence was of lesser importance to the lakes, and sodium and chloride contributed to factor 4, together with the drainage area to lake surface area ratio. Factor 2 in Labrador comprised several variables, but because it was most highly correlated with dissolved organic carbon (DOC) and colour, and negatively correlated with both maximum and mean depth, it might be regarded as a dystrophy factor. The third factor in Labrador had strong positive correlations with maximum and mean depth, lake surface area, and drainage area. Factor 3 in both Newfoundland and New Brunswick – Nova Scotia represented dystrophy-related elements with contributions from metals, colour, or DOC and, in the latter region, negative maximum depth. The fourth factor in Newfoundland was correlated negatively with metals, turbidity, and colour and positively with maximum depth and nitrate, while factor 5 was strongly positive for drainage areas and drainage area to lake surface area ratio. Factor 4 in New Brunswick – Nova Scotia was correlated with only potassium and maximum depth.

In summary, the factor relating to buffering capacity was of greatest importance in all three regions. The marine factor was also important in Newfoundland and New Brunswick – Nova Scotia, explaining about 18% of the variance, but less so in Labrador where lakes were generally more distant from the ocean. The high variance explained by factor 2 in Labrador (23.0%) suggests that colour, turbidity, and depth may be as valuable as pH or alkalinity for distinguishing lakes in this region.

Zooplankton and the Derived Factors

We identified 62 species: 32 rotifers, 19 cladocerans, and 11 copepods (Table 2). There were marked regional differences in zooplankton assemblages. Only 26 species (42%) were common to all three regions, which is not surprising considering the large area covered (over 15° latitude) and the partial isolation of each region. Labrador was particularly poor in copepod species with only four, but numbers of rotifer and cladoceran species were roughly equal among regions.

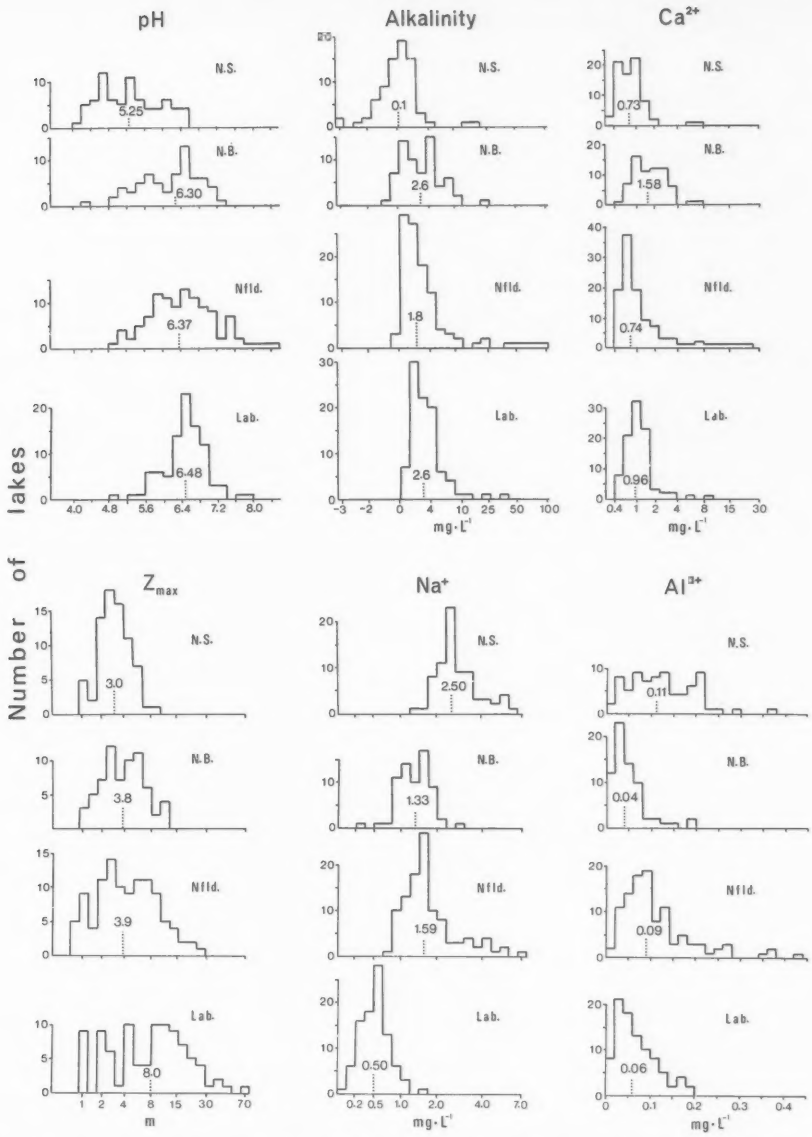


FIG. 1. Frequency distributions of lakes in Nova Scotia, New Brunswick, Newfoundland, and Labrador in relation to six chemical and morphometric variables. Medians are indicated by dotted lines. Note some scales are logarithmic.

The Labrador species assemblages exhibited little structure; i.e. only a single pair of rotifers, *Kellicottia bostoniensis* and *Keratella cochlearis*, were correlated in their abundance (Fig. 2). The species appeared to be independently distributed among lakes, and they showed few strong rank correlations with the lake factors. Only *Daphnia galeata mendotae* was strongly correlated with factor 1 (buffering), while two rotifers, *Ascomorpha ecaudis* and *Gastropus stylifer*, were negatively correlated with factor 2 (dystrophy). We failed to detect any strong correlations between the derived factors and the totals and conclude that water chemistry and morphometry have little influence in determining abundances of either species or individuals in Labrador lakes (Table 3).

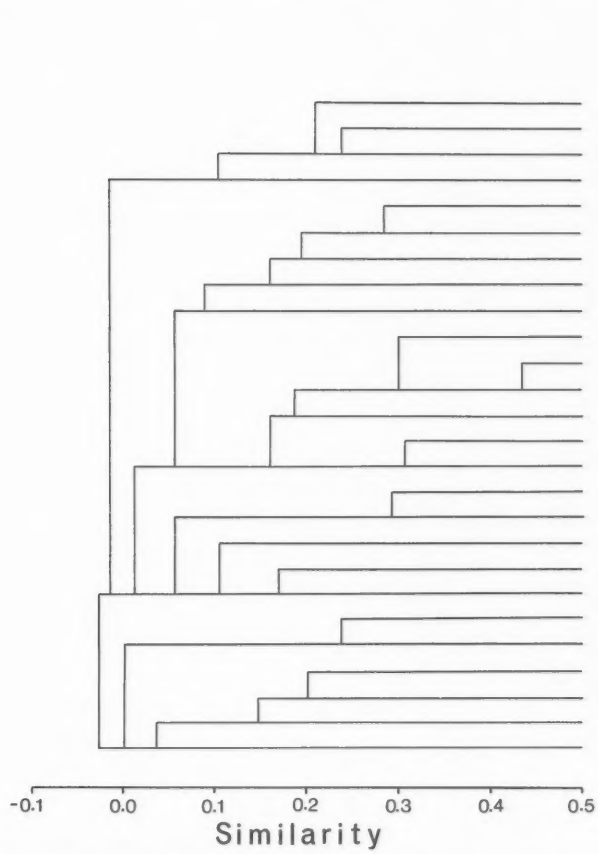
The Newfoundland zooplankton species showed slightly more pattern (Fig. 3). A number of species were clustered at >0.3 on the similarity index, while the whole was split into two clusters of approximately equal numbers. The upper cluster, from *Asplanchna priodonta* to *Polyarthra euryptera*, consisted almost exclusively of small species, including 10 rotifers, the smallest cladoceran (*Bosmina longirostris*), and *Cyclops scutifer* (a deepwater species). The lower cluster, from *Conochilus unicornis* to *Mesocyclops edax*, contained almost all of the larger forms, including eight crustaceans and one colonial rotifer (*C. unicornis*). Because selection by plank-

TABLE 2. Zooplankton species from the three regions with number of lakes of occurrence. Total lakes sampled in each region bracketed.

Species	Labrador (93)	Newfoundland (107)	New Brunswick – Nova Scotia (142)
Rotifera			
Ascomorpha ecaudis	16		5
Asplanchna priodonta	29	24	33
Bipalpus hudsoni	4	7	6
Collotheca libera	12		
Collotheca mutabilis	31	30	7
Conochiloides natans	6		
Conochilus unicornis	92	80	55
Euchlanis dilatata	2		
Gastropus stylifer	79	61	33
Kellicottia bostoniensis	10	13	12
Kellicottia longispina	92	96	69
Keratella cochlearis	89	75	52
Keratella crassa	10	14	61
Keratella earlinae		7	
Keratella hiemalis	5		
Keratella quadrata		1	
Keratella taurocephala	20	94	116
Notholca squamula			1
Ploesoma lenticulare	1	36	33
Ploesoma truncatum	3	1	2
Polyarthra dolichoptera	14	31	68
Polyarthra euryptera		15	3
Polyarthra major	19	17	14
Polyarthra minor			5
Polyarthra vulgaris	73	14	25
Synchaeta oblonga	6		
Synchaeta pectinata		9	5
Synchaeta stylata		4	
Trichocerca cylindrica	25	44	48
Trichocerca multicrinis		8	19
Trichocerca pusilla	10		
Trichocerca similis			4
Cladocera			
Bosmina longirostris	20	35	74
Ceriodaphnia lacustris	1	6	26
Chydorus brevilabris	14	5	
Chydorus sphaericus		2	
Daphnia catawba	6	80	58
Daphnia dubia	3		13
Daphnia galeata mendotae	18		
Daphnia laevis			3
Daphnia longiremis	49		
Daphnia parvula			3
Daphnia pulex	38		
Daphnia retrocurva			26
Diaphanosoma birgei		25	127
Eubosmina longispina	76	77	68
Eubosmina tubicen			56
Holopedium gibberum	79	65	99
Leptodora kindtii	6	7	35
Polyphemus pediculus		2	17
Sida crystallina		2	9
Copepoda			
Acanthocyclops vernalis			19
Cyclops scutifer	45	81	2
Mesocyclops edax		12	121
Orthocyclops modestus			1
Tropocyclops prasinus mexicanus		1	62
Diaptomus minutus	92	104	141

TABLE 2. (*Concluded*)

Species	Labrador (93)	Newfoundland (107)	New Brunswick – Nova Scotia (142)
Diaptomus pygmaeus			21
Diaptomus spatulocrenatus	2	20	41
Epischura lacustris	73	55	34
Epischura nordenskioldi		1	39
Eurytemora affinis		2	



	r_s with factor 1	2	3	4
A. ecaudis	0.08	-0.34★	0.06	-0.02
D. minutus	-0.18	-0.25	0.19	-0.08
E. longispina	0.01	-0.20	0.12	0.13
C. brevilabris	-0.08	-0.15	-0.11	-0.07
A. priodonta	0.11	-0.24	-0.01	-0.06
C. unicornis	-0.05	-0.25	-0.06	0.16
H. gibberum	0.02	-0.16	-0.01	-0.10
C. scutifer	0.09	-0.31	0.04	-0.08
C. mutabilis	-0.10	-0.30	0.07	0.07
G. stylifer	0.06	-0.34★	0.07	-0.13
K. longispina	0.13	-0.23	0.20	0.01
K. cochlearis	0.01	-0.05	0.22	0.04
P. vulgaris	0.24	-0.18	0.18	0.11
P. dolichoptera	0.10	-0.03	0.07	0.01
T. pusilla	0.11	-0.07	-0.04	-0.01
C. libera	0.01	-0.06	0.26	-0.27
D. g. mendotae	0.36★	0.04	0.19	0.32
E. lacustris	0.28	0.11	0.16	-0.09
B. longirostris	-0.21	0.05	-0.04	-0.09
D. longiremis	-0.05	0.06	0.17	-0.02
K. bostoniensis	-0.19	0.13	-0.09	-0.04
D. pulex	-0.07	0.15	-0.04	-0.08
K. crassa	-0.12	0.24	-0.15	0.01
T. cylindrica	0.05	0.17	0.02	-0.17
P. major	-0.22	0.04	0.22	0.06
K. taurocephala	0.14	0.21	0.17	0.09

FIG. 2. Dendrogram of zooplankton species in Labrador based on UPGMA, and Spearman rank correlation coefficients between each species and each of the four derived factors. Cophenetic correlation coefficient of dendrogram was 0.57. Asterisk indicates $p < 0.001$.

tivorous fish is often positively related to prey size (Hrbáček 1962; Brooks and Dodson 1965; Gardner 1981), possibly species in the lower cluster were concentrated in lakes with reduced predation pressure. On the other hand, as the lower group included *Epischura lacustris*, a major predator on *B. longirostris* (Kerfoot 1977; 1978), and *M. edax*, whose diet includes both *Bosmina* and rotifers (Williamson and Magnien 1982), perhaps the small zooplankters of the upper cluster dominated in lakes where predators from the lower cluster were absent or scarce (see Zaret 1980). Support for this latter hypothesis is that certain piscine planktivores (e.g. lake chub, *Couesius plumbeus*, lake whitefish, *Coregonus clupeaformis*, round whitefish, *Prosopium cylindraceum*) are absent from Newfoundland (Scott and Crossman 1973) and this may reduce predation pressure on invertebrate predators in many lakes.

Correlations between Newfoundland species and the first three factors were all weak, suggesting that water chemistry is unimportant in determining distributions. Four crustaceans were significantly correlated with factor 4, one negatively and three positively. As the strongest components of this factor were maximum depth and negative turbidity, it is probable that these correlations are chiefly related to lake morphometry and water transparency. Factor 5 included two more significant correlations, but these are difficult to interpret unless a large

TABLE 3. Spearman rank correlation coefficients between the derived factors and numbers of individuals and species within each of the three major taxonomic groups and in total in Labrador, Newfoundland, and New Brunswick – Nova Scotia. Asterisk indicates $p < 0.001$.

	Labrador				Newfoundland					New Brunswick – Nova Scotia			
	1	2	3	4	1	2	3	4	5	1	2	3	4
Individuals													
Rotifera	0.01	−0.23	0.03	0.08	−0.02	0.17	−0.33*	−0.01	−0.07	0.24	0.24	−0.01	0.25
Copepoda	−0.15	−0.31	0.23	−0.07	−0.19	0.12	−0.07	0.50*	−0.11	−0.15	−0.04	−0.14	0.22
Cladocera	−0.03	−0.13	0.01	−0.04	0.16	0.12	−0.18	0.23	0.01	0.03	0.08	0.24	0.23
Total	−0.06	−0.26	0.02	0.09	−0.06	0.20	−0.25	0.18	−0.09	0.06	−0.11	0.03	0.24
Species													
Rotifera	−0.01	−0.06	0.18	−0.07	0.11	0.11	−0.14	−0.01	0.12	0.42*	−0.19	−0.14	0.28*
Copepoda	0.24	−0.31*	0.01	0.10	0.27	−0.26	0.09	0.23	0.16	0.31*	−0.15	0.04	0.28*
Cladocera	−0.02	0.05	0.17	−0.27	0.11	−0.25	−0.06	0.29	0.10	0.28*	−0.10	−0.02	0.32*
Total	0.08	−0.13	0.22	−0.12	0.24	−0.10	−0.09	0.15	0.19	0.43*	−0.19	−0.07	0.38*

TABLE 4. Results of discriminant analysis of New Brunswick – Nova Scotia lakes. Numbers and percentages (in parentheses) of lakes predicted by the analysis to lie within each of three previously designated groups.

Group	No. of lakes	1	2	3	Overall
1	48	42 (87.5)	6 (12.5)	0 (0.0)	
2	46	8 (17.4)	32 (69.6)	6 (13.0)	
3	48	0 (0.0)	10 (20.8)	38 (79.2)	
Overall	142				112 (78.9)

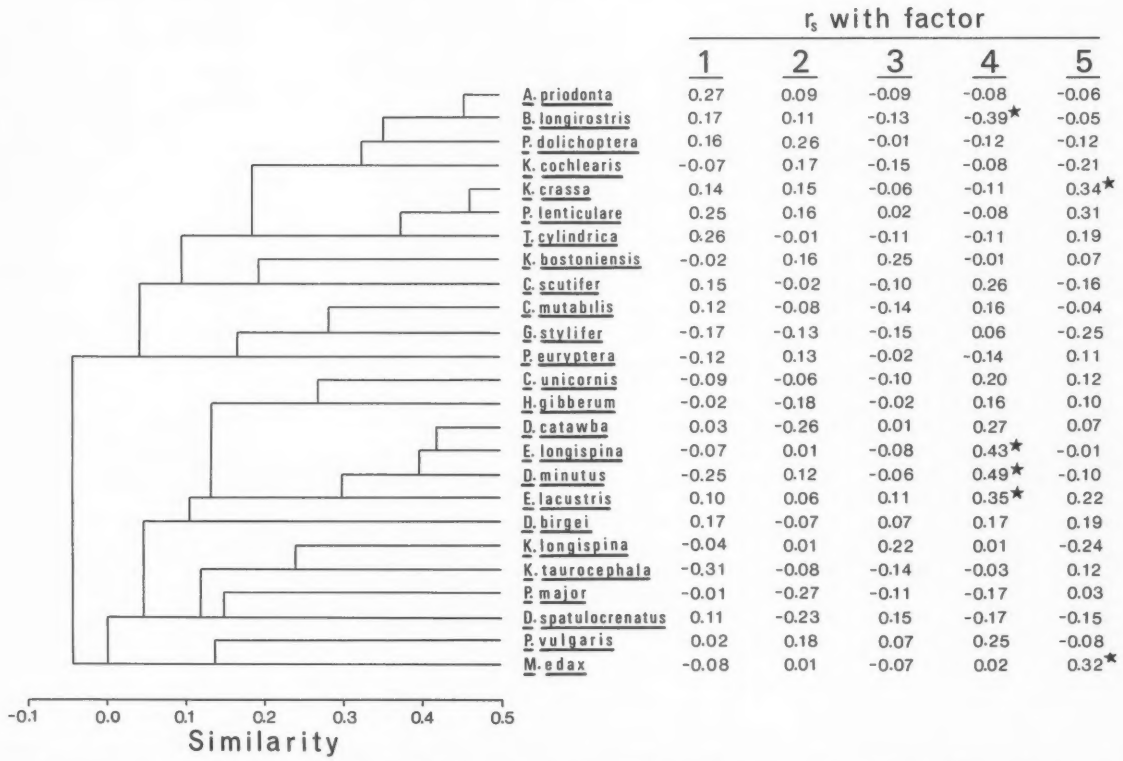
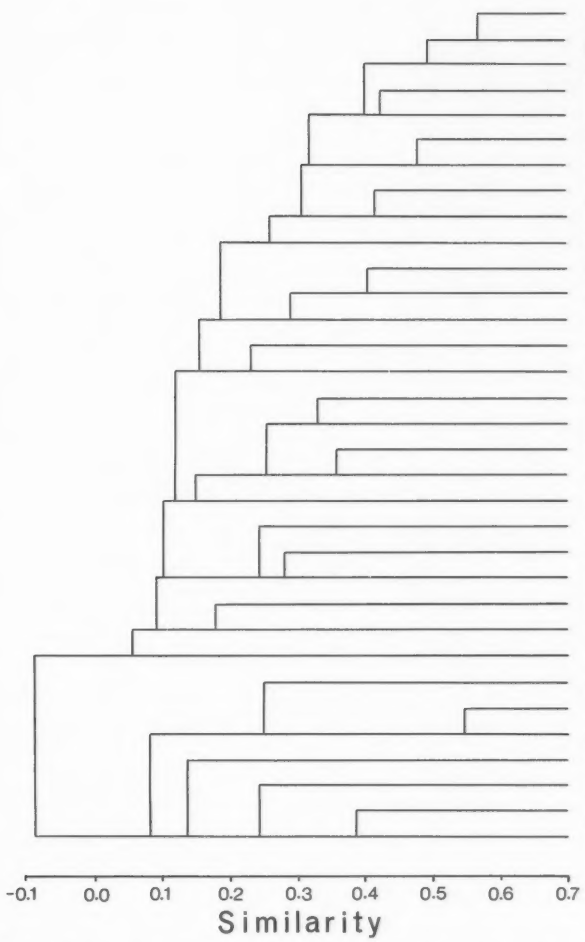


FIG. 3. Dendrogram of zooplankton species in Newfoundland based on UPGMA, and Spearman rank correlation coefficients between each species and each of the five derived factors. Cophenetic correlation coefficient of dendrogram was 0.66. Asterisk indicates $p < 0.001$.



	r_s with factor			
	1	2	3	4
A. priodonta	0.31*	-0.35*	0.16	-0.01
K. crassa	0.39*	-0.20	-0.01	0.18
K. cochlearis	0.28*	-0.15	-0.03	0.05
T. multicrinis	0.16	-0.16	-0.01	0.10
A. vernalis	0.38*	-0.36*	0.04	0.13
D. retrocurva	0.49*	-0.42*	0.04	0.21
C. lacustris	0.37*	-0.22	0.13	0.04
P. dolichoptera	0.46*	-0.18	0.11	0.20
T. p. mexicanus	0.44*	-0.13	0.07	0.26
G. stylifer	0.21	-0.26	-0.05	0.17
K. longispina	0.53*	-0.02	-0.20	0.29*
E. lacustris	0.39*	-0.24	-0.16	0.20
T. cylindrica	0.45*	-0.20	-0.15	0.15
P. lenticulare	0.15	-0.31*	-0.15	0.25
L. kindtii	0.10	-0.24	-0.15	0.20
P. major	-0.02	0.15	0.14	0.14
E. tubicen	0.18	0.08	0.04	0.34*
M. edax	0.23	-0.09	-0.03	0.21
B. longirostris	0.23	-0.14	-0.14	0.09
D. dubia	0.20	0.08	0.13	0.09
C. unicornis	0.12	-0.06	-0.13	0.08
H. gibberum	-0.02	0.01	0.01	0.14
D. birgei	0.21	0.02	0.19	0.21
K. bostoniensis	0.03	-0.01	0.11	0.11
D. pygmaeus	0.07	0.14	0.17	-0.07
P. pediculus	0.01	-0.02	-0.21	0.18
K. taurocephala	-0.47*	0.16	-0.05	-0.06
E. nordenskiöldi	-0.49*	0.41*	0.22	-0.07
E. longispina	-0.55*	0.35*	-0.02	-0.16
P. vulgaris	0.12	0.07	0.12	0.10
D. minutus	-0.26	0.03	-0.10	0.17
D. spatulocrenatus	0.05	-0.10	0.08	0.15
D. catawba	0.06	0.12	-0.09	0.02

FIG. 4. Dendrogram of zooplankton species in New Brunswick – Nova Scotia based on UPGMA, and Spearman rank correlation coefficients between each species and each of the four derived factors. Cophenetic correlation coefficient of dendrogram was 0.79. Asterisk indicates $p < 0.001$.

drainage area and high drainage area to lake surface area ratio is explained as evidence of heavier than average phosphorus loadings. In any event, factors 4 and 5 explain only 9.9 and 5.4% of the total variance, respectively (Table 1).

Total individual rotifers in Newfoundland lakes were significantly negative to factor 3 (dystrophy), while total individual copepods showed a strong positive correlation with factor 4 (maximum depth and negative turbidity) (Table 4). This suggests that both rotifers and copepods have higher abundances in more transparent waters. Correlations between the environmental factors and total species for all three major taxa were weak.

The New Brunswick – Nova Scotia fauna contained many moderately high correlations (>0.3), but also a relatively clear separation of the lower seven species on the dendogram from those above (Fig. 4). Eleven species in the top half of the upper cluster showed positive Spearman correlations with factor 1, while three species in the lower cluster were significantly negative. A number of these correlations were comparatively strong ($r_s > 0.45$). Clearly, the zooplankton composition of New Brunswick – Nova Scotia lakes is related to one or more of the variables comprising factor 1. Five of the 14 species sensitive to factor 1 were also correlated significantly with factor 2 (salinity), but with the opposite sign. From this we infer that some species correlating positively with factor 1 were mainly from inland lakes, while some of those correlating negatively were concentrated in lakes nearer the sea. Two species were also significantly related to factor 4 (potassium and depth). Total species number, but not total number of individuals, was significantly correlated with factors 1 and 4 for all three taxonomic groups (Table 3). This will be discussed further.

In summary, the Labrador lakes showed no evidence of

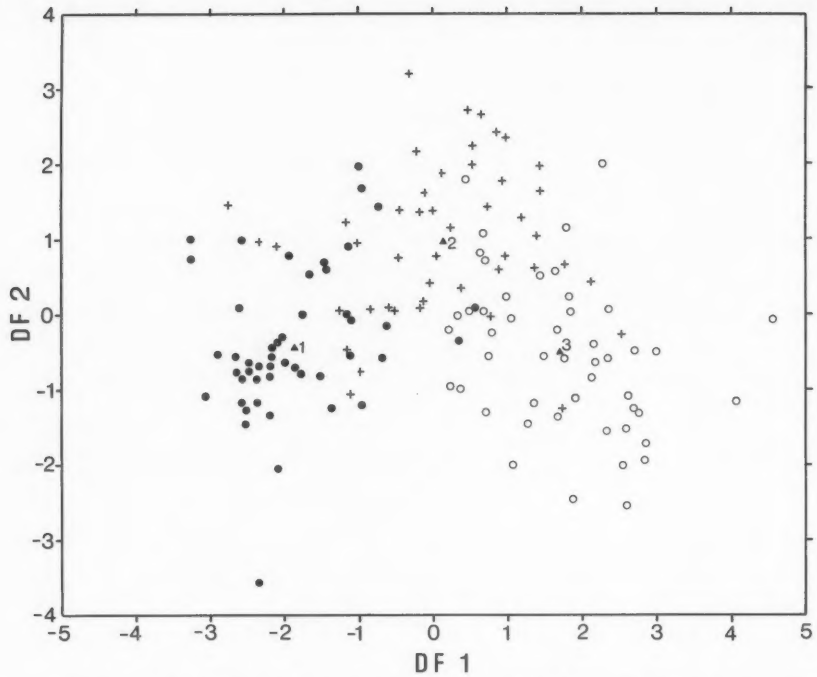


FIG. 5. Separation of the three New Brunswick – Nova Scotia lake groups on the two discriminant functions. ●, group 1 (acidic lakes); +, group 2 (intermediate lakes); ○, group 3 (nonacidic lakes).

segregation of species into distinct communities, and we conclude that distribution of species was essentially independent. Even the wide range of lake depths was ineffective in producing species groups. One reason for this is undoubtedly that the eastern extremity of North America, because of its unique glacial history, contains no deepwater relicts (Dadswell 1974; Carter et al. 1980) and consequently the zooplankton is almost entirely epilimnetic or metalimnetic. Secondly, the absence of any significant correlations with the derived buffering factor suggested that acidification was not affecting the zooplankton in this region. The situation with regard to Newfoundland lakes was very similar, and for much the same reasons, although here there was some evidence of an interesting separation into two types of community based on invertebrate and/or vertebrate predation.

However, the results for New Brunswick – Nova Scotia show a different picture; numerous low values of pH and alkalinity (Fig. 1) and strong correlations within clustered species to factor 1 (Fig. 4) suggest that acidification may be affecting limnetic zooplankton in this region.

Classification of New Brunswick – Nova Scotia Lakes

Encouraged by the strong relationship to factor 1 of the New Brunswick – Nova Scotia zooplankton species, we reasoned that the lakes in this region, and possibly those in Newfoundland also, might cluster on the basis of their zooplankton. However, this was not the case; the dendograms (not shown) were highly complex, without obvious clusters, and for the most part unamenable to interpretation. We conclude that, although some lake types probably did contain similar species assemblages, these assemblages intergraded.

We then considered whether or not lakes in New Brunswick – Nova Scotia with low and high scores on factor 1 (the buffering factor; Table 1) could be distinguished on the basis of their zooplankton fauna. The 142 lakes were divided into three approximately equal-sized groups on the basis of their factor 1 score: group 1 with the lowest scores, group 2 with intermediate scores, and group 3 with the highest scores. Multiple discriminant analysis demonstrated that the lakes in these groups could be recognized on the basis of their fauna (Table 4).

Three groups of lakes emerged following ordination based on the first and second discriminant functions (Fig. 5). They account for 82.6 and 17.4% of the variance, respectively, and function 2 is largely a "horseshoe effect" (Fasham 1977). As expected, group 2 extensively overlaps both groups 1 and 3, but the latter are almost completely separated. Discriminant function coefficients, indicating the taxa most useful in separating the lake types, are given in Table 5.

Group 1 lakes, with very few exceptions, are situated around the Bay of Fundy in southern New Brunswick and southwest Nova Scotia (Fig. 6). With the lowest factor 1 scores, they were defined by the factor analysis (Table 1) as low in pH, alkalinity, calcium, and magnesium and will be called the "acidic" lakes. Group 3 lakes are mainly in western and northern New Brunswick with a scatter throughout Nova Scotia. They have the highest factor 1 scores, and will be called the "nonacidic" lakes. Group 2, the "intermediate" lakes, are widely distributed but many are in southern New Brunswick and central Nova Scotia.

The detailed geology of each lake basin or lake drainage area was not determined at the time of sampling. Nevertheless, by

TABLE 5. Disciminant analysis of New Brunswick – Nova Scotia lakes. Standardized canonical discriminant function coefficients.

Species	Function 1	Function 2
K. longispina	0.457	0.114
C. lacustris	0.376	0.032
T. cylindrica	0.355	0.060
D. retrocurva	0.272	−0.344
E. lacustris	0.259	−0.130
T. p. mexicanus	0.250	0.060
K. crassa	0.132	−0.100
D. dubia	0.103	0.143
D. birgei	0.096	0.137
P. dolichoptera	0.091	0.040
P. lenticulare	0.087	−0.100
K. cochlearis	0.071	0.057
P. major	0.064	0.361
M. edax	0.056	0.198
D. catawba	0.036	0.233
G. stylifer	0.013	0.341
D. spatulocrenatus	−0.001	0.165
K. bostoniensis	−0.003	0.032
E. nordenskioldi	−0.005	0.049
A. priodonta	−0.018	0.195
B. longirostris	−0.043	0.177
P. vulgaris	−0.074	0.250
A. vernalis	−0.085	−0.035
C. unicornis	−0.016	−0.081
D. minutus	−0.119	0.033
H. gibberum	−0.131	−0.251
D. pygmaeus	−0.157	−0.061
P. pediculus	−0.190	−0.347
E. tubicen	−0.218	0.041
K. taurocephala	−0.256	0.119
L. kindtii	−0.306	−0.137
T. multicrinis	−0.317	−0.388
E. longispina	−0.496	−0.098

reference to Fig. 7 it is possible to identify some lake groupings in Fig. 6 according to the predominant rock type of the regions they occupy. Most of the lakes in New Brunswick are in either Precambrian sedimentary or granitic formations. The exceptions include five from group 3 near the mouth of the St. Croix River (Devonian granite or Devonian gabbro-diorite) and a series of five from groups 2 and 3 located near the Fundy coast and near the mouth of the St. John River (sedimentary Triassic rock) (R. H. Peterson, DFO, St. Andrews, N.B. E0G 2X0, pers. comm.). In Nova Scotia a slightly higher proportion either lie in, or drain from, sedimentary deposits, but the great majority were specifically chosen from regions of metamorphic rock, chiefly in the southwestern part of the province.

Sources and Biological Effects of Acidification

The Bay of Fundy region possesses two features which might accelerate the process of lake acidification: it lies within the southwest-to-northeast summer air flow carrying atmospheric pollutants from centres along the American Atlantic seaboard, and it is an area of higher than average precipitation and fog (Putnam 1940). The latter scavenges ions from polluted air masses and hastens their deposition on soils and surface waters. For 1980, the latest year available, values for wet deposition of hydrogen, sulphate, and nitrate ions were higher in the general Bay of Fundy region than elsewhere in the two provinces (Fig. 8). Which of sulphate and nitrate is the major source of acidification of the environment is still disputed, but that both contribute is no longer questioned (D. M. Whelpdale, Atmospheric Environment Service, Environment Canada, Downsview, Ont. M3H 5T4, pers. comm.).

Possibly many of the more sensitive lakes in New Brunswick – Nova Scotia have been acidic for much of the recent past. While their waters are very dilute, they also contain high amounts of organic carbon and sulphate ion, the latter probably released from bogs (Kerekes et al. 1982).

The primary attribute of acidic lakes in New Brunswick – Nova Scotia was a lower species richness for all three taxonomic groups (Table 3). It must be emphasized that numbers of species declined, not that species were eliminated when the pH fell below certain values. In the 12 lakes with pH $\leq$ 4.5, the ranges in species numbers were one to seven rotifers, two to five cladocerans, and two to four copepods. Without exception, all previous studies have reported a decline in numbers of rotifer species with pH (Almer et al. 1974; Roff and Kwiatkowski 1977; Brezonik et al. 1984; Siegfried et al. 1984). The dominant acidophilic rotifer in our lakes was *Keratella taurocephala* (Fig. 4) which was present in all of the 12 lakes noted above. Its acid preferences have been noted by others (Chengalath and Fernando 1973; Siegfried et al. 1984). Rotifers showing strong positive correlations with factor 1, and hence more common in nonacidic lakes, were *A. priodonta*, *Keratella crassa*, *K. cochlearis*, *Polyarthra dolichoptera*, and *Trichocerca cylindrica*. In Europe, *K. cochlearis* and *T. cylindrica* are considered as indicators of eutrophic waters (Pejler 1957; Dumont 1977; Maemets 1983).

Crustacean species abundance has not always been so closely correlated with pH. Some studies (e.g. Carter 1971; Sprules 1975; Fryer 1980; Confer et al. 1983) have noted declines in both cladocerans and copepods; in others, the results have been less conclusive (e.g. Roff and Kwiatkowski 1977; Brezonik et al. 1984). *Eubosmina longispina* was the major cladoceran of the acidic lakes and occupied 11 of 12 lakes of pH $\leq$ 4.5. *Daphnia retrocurva* and *Ceriodaphnia lacustris* were most positively correlated with factor 1 of all cladocerans, and were completely excluded from more acid waters. Among copepods, *Epischura nordenskioldi* was found only in waters of low pH, mainly in Nova Scotia. Its congener, *E. lacustris*, was significantly positive to factor 1, as were the two cyclopoids *Acanthocyclops vernalis* and *Tropocyclops prasinus mexicanus*. The calanoid *Diaptomus minutus* was the most abundant and widespread of any zooplankter, inhabiting all but a single lake (Table 2). This suggests that presence or absence in acid waters may often be controlled largely by competition rather than any lethal effects of the water. Carter (1971) noted that at low pH, *D. minutus* was replaced by *D. reighardi*, a species confined to the St. Lawrence Great Lakes region.

Numbers of individuals in New Brunswick – Nova Scotia were not strongly correlated with factor 1 in any of the three major taxonomic groups, although rotifers showed a modest positive correlation (Table 3). Roff and Kwiatkowski (1977) and Brezonik et al. (1984) both found a reduction in total numbers at low pH, whereas Carter (1971) noted a marked increase. Probably a lake's trophic status is as important as pH in determining abundance, although the two variables are undoubtedly related.

Species in total and in each of the groups were also sig-

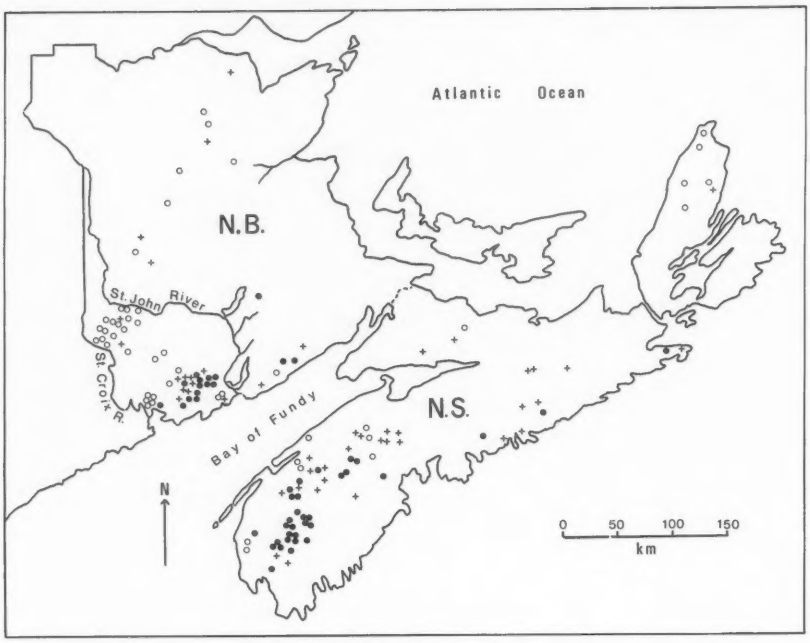


FIG. 6. Location of the New Brunswick – Nova Scotia lakes. ●, group 1 (acidic lakes); +, group 2 (intermediate lakes); ○, group 3 (nonacidic lakes).

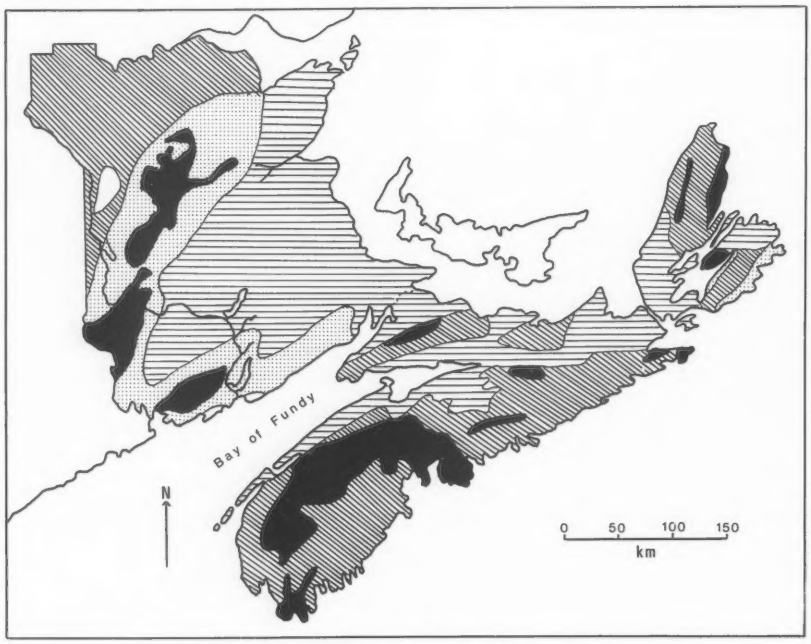


FIG. 7. Geology of New Brunswick and Nova Scotia. Horizontally hatched areas = sedimentary rocks with some volcanic rocks and gabbro sills, flat lying to partly deformed; diagonally hatched areas = sedimentary rocks with some volcanic rocks and gabbro sills, strongly deformed and metamorphosed; stippled area = grantic instrusions, granitic gneiss, magmatite, granulitic gneiss, charnockite. Redrawn from Energy, Mines and Resources Canada (1984).

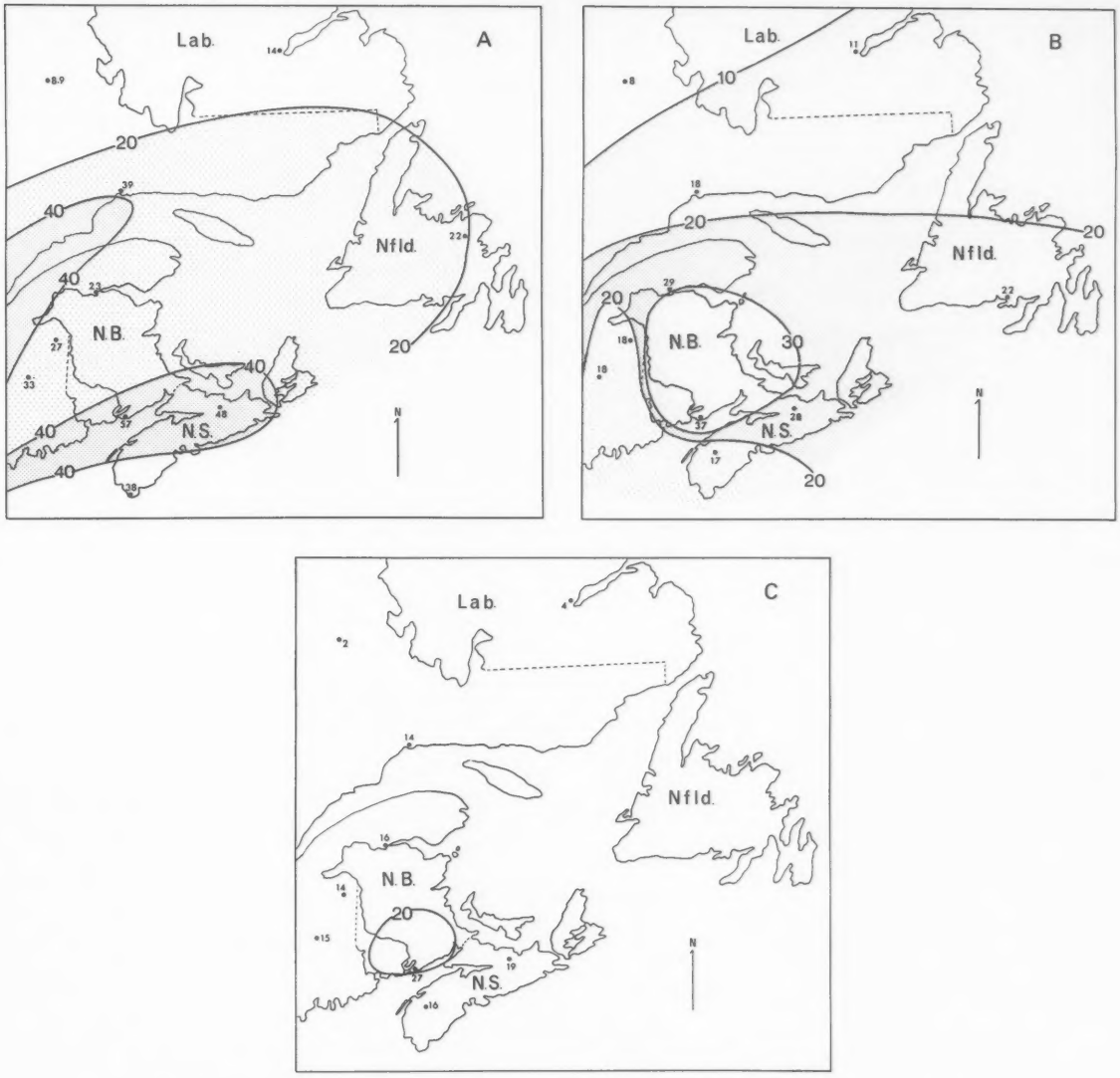


FIG. 8. Precipitation amount-weighted mean deposition for 1980 (mmol·m^{-2}) of (A) hydrogen ion, (B) sulphate ion, and (C) nitrate ion. Redrawn from Environment Canada (1982).

nificantly correlated with factor 4 (Table 3); because factor 4 includes maximum depth, this may simply mean that shallow lakes are more sensitive to acidification from atmospheric deposition because of their high surface area to volume ratio.

Zooplankton assemblages in maritime Canada generally showed few interspecific correlations suggestive of biological interactions, and species abundances were not commonly correlated with the chemical and morphological variables measured in this study. In Newfoundland, there is an indication that lakes differ in the relative intensity of vertebrate and invertebrate predation. However, in New Brunswick – Nova Scotia, weakly buffered lakes, largely in coastal areas, have distinct zooplankton communities with reduced species richness, suggesting that acidic precipitation has affected this area.

Acknowledgements

We thank J. Hines, University of Guelph, for undertaking some of the multivariate analyses and many members of the University of Waterloo Biology Department for their constructive comments and criticism. Dr. John Roff, University of Guelph, did an outstanding job reviewing the manuscript. The study was made possible by contracts from the Department of Fisheries and Oceans to J. C. H. Carter and operating grants from the Natural Sciences and Engineering Research Council of Canada to J. C. H. Carter and W. D. Taylor.

References

ALMER, B., W. DICKSON, C. EKSTROM, E. HORNSTROM, AND U. MILLER. 1974. Effects of acidification on Swedish lakes. Ambio 3: 30–36.

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, Washington, DC. 874 p.

BREZONIK, P. L., T. L. CRISMAN, AND R. L. SCHULZE. 1984. Planktonic communities in Florida softwater lakes of varying pH. Can. J. Fish. Aquat. Sci. 41: 46–56.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size and composition of the plankton. Science (Wash., DC) 150: 28–35.

CARTER, J. C. H. 1971. Distribution and abundance of planktonic Crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. Arch. Hydrobiol. 68: 204–231.

CARTER, J. C. H., M. J. DADSWELL, J. C. ROFF, AND W. G. SPRULES. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. Can. J. Zool. 58: 1355–1387.

CHENGALATH, R., AND C. H. FERNANDO. 1973. The planktonic Rotifera of Ontario with records of distribution and notes on morphological variation. Can. Field-Nat. 87: 267–277.

CONFER, J. L., T. KAARET, AND G. E. LIKENS. 1983. Zooplankton diversity and biomass in recently acidified lakes. Can. J. Fish. Aquat. Sci. 40: 36–42.

DADSWELL, M. J. 1974. Distribution, ecology and postglacial dispersion of certain crustaceans and fishes in eastern North America. Natl. Mus. Can. Publ. Zool. 11: 110 p.

DUMONT, H. J. 1977. Biotic factors in the population dynamics of rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 98–122.

ENERGY, MINES AND RESOURCES CANADA. 1984. Map 900 A. 34th ed. Mineral Policy Sector and Geological Survey of Canada, Ottawa, Ont.

ENVIRONMENT CANADA. 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

1982. United States – Canada Memorandum of Intent on Transboundary Air Pollution. Air Quality and Inter-Environmental Research Branch, Atmospheric Environment Service, Ottawa, Ont.

FASHAM, M. J. R. 1977. A comparison of non-metric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines, and coenoplanes. Ecology 58: 551–561.

FRYER, G. 1980. Acidity and species diversity in freshwater crustacean faunas. Freshwater Biol. 10: 41–45.

GARDNER, M. B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of a hypothesis. Ecology 62: 571–578.

HAINES, T. A. 1981. Acid precipitation and its consequences: A review. Trans. Am. Fish. Soc. 110: 669–707.

HRBÁČEK, J. 1962. Species composition and the amount of the zooplankton in relation to the fish stock. Rozpravy Ceskosl. Adad. Ved. Rada Matem. Prir. Ved. 72: 1–114.

KELLER, W., AND J. R. PITBLADO. 1984. Water quality – crustacean plankton relationships in northeastern Ontario lakes. Water Air Soil Pollut. 23: 271–291.

KEREKES, J., G. HOWELL, S. BEAUCHAMP, AND T. POLLOCK. 1982. Characterization of three lake basins sensitive to acid precipitation in central Nova Scotia (June, 1979, to May, 1980). Int. Rev. Gesamten Hydrobiol. 67: 679–694.

KERFOOT, W. C. 1977. Implications of copepod predation. Limnol. Oceanogr. 22: 316–325.

1978. Combat between predatory copepods and their prey: *Cyclops*, *Epischura* and *Bosmina*. Limnol. Oceanogr. 23: 1089–1102.

LEGENDRE, L., AND P. LEGENDRE. 1983. Numerical ecology. Elsevier Scientific Publications Co., Amsterdam. 419 p.

MAEMETS, A. 1983. Rotifers as indicators of lake types in Estonia. Hydrobiologia 104: 357–361.

ONTARIO MINISTRY OF THE ENVIRONMENT. 1979. Determination of the susceptibility to acidification of poorly buffered surface waters. Water Resources Branch, Limnology and Toxicity Section, Rexdale, Ont. 21 p.

ONTARIO MINISTRY OF NATURAL RESOURCES. 1980. Determination of total inflection point alkalinity. Instruction manual for sampling and field titration. Fisheries Branch, Environmental Dynamics Division, Toronto, Ont. 35 p.

PATALAS, K. 1971. Crustacean plankton communities in forty-five lakes in the experimental lakes area, northwestern Ontario. J. Fish. Res. Board Can. 28: 231–244.

PEJLER, B. 1957. Taxonomical and ecological studies on planktonic Rotatoria from central Sweden. Kungl. Svensk. Vet. Akad. Handl. 6: 1–52.

PUTNAM, D. F. 1940. The climate of the maritime provinces. Can. Geogr. J. 21: 135–147.

ROFF, J. C., AND R. E. KWIATKOWSKI. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board. Can. 184: 966 p.

SCRUTON, D. A. 1983. A survey of headwater lakes in insular Newfoundland, with special reference to acid precipitation. Can. Tech. Rep. Fish. Aquat. Sci. 1195: 110 p.

1984. A survey of selected lakes in Labrador, with an assessment of lake status and sensitivity in relation to acid precipitation. Can. Tech. Rep. Fish. Aquat. Sci. 1296: 115 p.

SIEGFRIED, C. A., J. W. SUTHERLAND, S. O. QUINN, AND J. A. BLOOMFIELD. 1984. Lake acidification and the biology of Adirondack lakes: I. Rotifer communities. Verh. Int. Ver. Limnol. 22: 549–558.

SPRULES, W. G. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. J. Fish. Res. Board Can. 32: 389–395.

WATT, W. D., D. SCOTT, AND S. RAY. 1979. Acidification and other chemical changes in Halifax County lakes after 21 years. Limnol. Oceanogr. 24: 1154–1161.

WILLIAMSON, C. E., AND R. E. MAGNIEN. 1982. Diel vertical migration in *Mesocyclops edax*: implications for predation rate estimates. J. Plankton Res. 4: 329–339.

WILTSHIRE, J. F., AND J. R. MACHELL. 1981. A study of acidification in sixteen lakes in mainland Nova Scotia and southern New Brunswick. Environment Canada, Environmental Protection Service, Atlantic Region, Halifax, N.S. EPS5-AR-81-4: 102 p.

YAN, N. D., AND R. STRUS. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293.

ZARET, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT. 187 p.

Effects of Density-Dependent and Climatic Factors on American shad, *Alosa sapidissima*, Recruitment: A Predictive Approach

Victor Crecco and Thomas Savoy

State of Connecticut, Department of Environmental Protection, P.O. Box 248, Waterford, CT 06385, USA

and Walter Whitworth

Department of Renewable Natural Resources, University of Connecticut, Storrs, CT 06468, USA

Crecco, V., T. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: a predictive approach. Can. J. Fish. Aquat. Sci. 43: 457–463.

We developed environment-dependent stock–recruitment models for American shad, *Alosa sapidissima*, in the Connecticut River to forecast recruitment variability and measure density-dependent effects. These models were fitted to the 1966–78 stock–recruitment estimates and to May and June river flow, water temperature, and rainfall data shown previously to affect American shad year-class strength. We also attempted to validate the models by forecasting the 1979–84 year-classes based on juvenile indices, parent stock size, and hydrographic data for these years. The stock–recruitment models without environmental factors explained less than 3% of the recruitment variability, and none of the density-dependent exponents were statistically different from 0. The predictive capability of the Ricker stock–recruitment model improved dramatically ($r^2 = 0.90$) when combined with mean May flows, June flows, and the number of American shad lifted over the Holyoke Dam. The density-dependent exponents of these multiple regression models were highly significant, indicating that density-dependent processes are hidden by climatically induced variability in recruitment. Two environment-dependent stock–recruitment models predicted 80–90% of the American shad recruitment variability from 1979–84.

Les auteurs ont élaboré des modèles de relations stock–recrutement dépendantes de l'environnement pour l'alose (*Alosa sapidissima*) dans la rivière Connecticut afin de prévoir la variabilité du recrutement et de mesurer les effets dépendants de la densité. Les modèles ont été ajustés aux estimations de stock–recrutement de 1966 à 1978 ainsi qu'aux données relatives au débit de la rivière, à la température de l'eau et aux précipitations entre mai et juin, dont l'effet sur l'importance de la classe annuelle des aloses a déjà été démontré. Les auteurs ont aussi tenté de vérifier la validité des modèles par la prévision des classes annuelles de 1979 à 1984 à partir des indices des juvéniles, de la taille du stock parental et de données hydrographiques ayant trait à ces années. Les modèles de stock–recrutement utilisés sans facteurs environnementaux permettaient d'expliquer moins de 3 % de la variabilité du recrutement, et aucun des exposants dépendants de la densité ne différait statistiquement de 0. La capacité de prévision du modèle stock–recrutement de Ricker s'améliorait de façon extrêmement importante ($r^2 = 0{,}90$) quand on tenait aussi compte des débits moyens en mai et juin et du nombre d'aloses ayant passé le barrage Holyoke. Les exposants dépendants de la densité de ces modèles de régression multiple étaient fortement significatifs, ce qui montre que les processus dépendants de la densité sont obscurcis par la variabilité du recrutement induite par des facteurs climatiques. Deux modèles de stock–recrutement dépendants de l'environnement ont permis de prévoir de 80 à 90 % de la variabilité du recrutement de l'alose entre 1979 et 1984.

Received May 15, 1985
Accepted October 21, 1985
(J8245)

Reçu le 15 mai 1985
Accepté le 21 octobre 1985

It is widely accepted that density-dependent processes (cannibalism, predation, and starvation) play a major role in regulating fish population stability, especially when spawning stock size falls below or exceeds some threshold density (Ricker 1954; Beverton and Holt 1957; Cushing 1975). The density-dependent effects among exploited fish populations have been traditionally characterized by nonlinear stock–recruitment models (Ricker 1975; Shepard 1982). However, the stock–recruitment concept has had limited application to population dynamic studies of most marine and anadromous clupeid fishes because their recruitment levels are sensitive to hydrographic and meteorological perturbations (Craig 1960; Sutcliffe et al. 1977; Sinclair et al. 1982).

The effects of climatically induced variability on the stock–recruitment relationship for most clupeid fishes are not well understood (Cushing 1982). However, studies of American shad, *Alosa sapidissima*, in the Connecticut River showed that fluctuations in May and June river flow, temperature, and rainfall (Leggett 1977; Yoshiyama et al. 1981; Crecco and Savoy 1984) affect the rate at which shad eggs and larvae grow and develop (Marcy 1976; Crecco and Savoy 1985a), the mortality of larvae (Crecco et al. 1983), and the timing and duration of shad spawning (Leggett 1976). Given these hydrographic effects on recruitment, the predictive capability of stock–recruitment models can be improved greatly by incorporating the key climatic variables in environment-dependent stock–recruitment models (Nelson et al. 1977; Parrish and MacCall 1978; Stocker et al. 1985). We developed environment-dependent stock–recruitment models for American shad with the 1966–78 parent–progeny and May–June river flow, water temperature, and rainfall data. These models were designed to predict American shad recruitment variability

TABLE 1. Recruitment from juvenile relative abundance indices (RJ) and Holyoke population estimates (RH). Explanatory variables are parent stock size (P), adjusted June temperatures (TEMP), American shad lifted (LF), mean June flow (JFW), mean May flow (MFW), and adjusted May–June rainfall (MJP) from 1966–84. RJ, RH, P, and LF are in thousands.

Year	RJ	RH	P	TEMP (°C)	LF	JFW ($m^3 \cdot s^{-1}$)	MFW ($m^3 \cdot s^{-1}$)	MJP (mm)
1966	—	388	115	20.9	6	246	566	210
1967	—	222	167	21.4	6	437	964	228
1968	—	118	202	20.5	7	603	547	158
1969	—	245	384	21.2	14	375	1005	148
1970	—	275	413	21.8	17	243	856	220
1971	—	491	424	21.1	20	203	1175	207
1972	—	215	167	22.0	11	616	1459	316
1973	—	154	111	20.6	5	534	897	203
1974	—	326	306	20.6	14	334	992	159
1975	—	280	247	21.8	23	379	627	180
1976	—	325	435	19.5	166	286	840	230
1977	—	620	157	22.4	112	250	542	257
1978	—	278	210	20.0	45	488	799	138
1979	294	—	247	20.8	87	448	905	74
1980	641	—	341	21.7	196	202	488	220
1981	240	—	293	20.8	143	313	513	118
1982	71	—	501	21.9	109	637	653	295
1983	395	—	423	20.3	185	336	1137	122
1984	195	—	661	20.0	245	661	1442	217

and measure how density-dependent effects change with spawning stock size. Finally, we attempted to validate these models by forecasting American shad recruitment from 1979–84 with parent stock sizes and May and June flows, temperatures, and rainfall for those years.

Methods

Recruitment and Parent Stock Estimates

We used year-class strength and parent stock sizes from 1966–84 based on population estimates (Table 1) derived by the number of American shad lifted at the Holyoke Dam fishway, Holyoke, Massachusetts (river km 128). These year-class strength estimates for 1966–78 were significantly correlated with the corresponding year-class strength estimates from commercial data (Crecco 1985) as well as with the 1966–78 juvenile indices of abundance (Crecco and Savoy 1985b). The stock and recruitment estimates from the commercial data were not used because the catchability coefficients for the commercial fishery were inversely related to shad population size (Crecco and Savoy 1985b) and thus underestimate the true variability in year-class strength of American shad.

The population of female American shad from 1966–84 was estimated by multiplying the total population estimate from the Holyoke fishlift by the sex ratio obtained from that year's commercial population estimates (Crecco et al. 1981, 1982). Only female American shad were used because the age-class structure and commercial landings of male American shad are biased by gill net selectivity and differential culling practices by commercial fishermen (Crecco et al. 1981). Recruitment (R) of female American shad from the 1966–78 year-classes (Table 1) was the total contribution of virgin female shad of those year-classes in the 1970–84 runs based on the age-class structure from previous studies (Leggett 1976; Jones et al. 1976; Crecco et al. 1984). Year-classes after 1978 could not be included, as they have not yet been fully recruited to the spawning population. Population estimates of female American shad were not derived prior to 1966 because sex ratio and age structure data were lacking.

The parent stock (P) was the annual population estimates of female American shad from the Holyoke lift (Table 1) minus that year's commercial catch. This procedure was necessary because the main spawning areas (river km 75–190) are located well upriver of the commercial fishing areas (Leggett 1976). There is a significant sport fishery for American shad in the Connecticut River (Leggett 1976), but we did not subtract sport catches to estimate parent stock size, because angler catches for the entire river are lacking from 1974–81.

Stock–Recruitment Analysis

One of the unresolved questions in fisheries management is the extent to which recruitment is related to parent stock size (Gulland 1977; Cushing 1982). We determined whether a parent–progeny relationship was statistically significant for American shad by fitting recruitment and spawning stock (P) data to the compensatory Ricker and Beverton–Holt models (Ricker 1975), and to the depensatory Clark–Ricker model as recommended by Parrish and MacCall (1978). The Ricker stock–recruitment model:

$$\mathrm{Rp} = AP \exp(bP),$$

where Rp = predicted recruitment, A = coefficient of density independence, and b = coefficient of density dependence, implies that recuitment reaches a maximum at some moderate parent stock size and then declines at high stock sizes due to density-dependent mortality. By contrast, the Beverton–Holt model:

$$\mathrm{Rp} = P/(A + bP)$$

suggests that recruitment rises to an asymptote at high parent

stock sizes. If recruitment drops sharply at lower stock sizes, the stock is said to exhibit depensatory density-dependent mortality, the main cause of which is nonrandom predation on a spatially heterogenous fish population (Clark 1974; Peterman et al. 1979). The Clark–Ricker model:

$$\mathrm{Rp} = AP \exp(bP + c/P)$$

suggests that recruitment reaches a maximum at some moderate parent stock size as in the Ricker model, and then declines at low parent stock size due to increased depensatory mortality (c).

The three stock–recruitment models were fitted to observed recruitment (R) with the nonlinear least square procedure (SAS 1982). The nonlinear method provided asymptotic standard errors with which to test whether the compensatory and depensatory exponents differed significantly from 0. We also plotted the multiplicative residuals (R/Rp) for each stock–recruitment model against predicted recruitment levels (Rp) and parent stock size (P) (Belsley et al. 1980). If the residual plots exhibited linear or curvilinear trends with Rp or P, that stock–recruitment model was deleted from further analysis. The stock–recruitment model yielding the most significant ($p < 0.05$) density-dependent exponent (b) and the highest r^2 value was then used in the environment-dependent stock–recruitment model.

We removed the recruitment variability attributed to climatic factors because it has often been suggested that climatically induced variability in recruitment could statistically mask a parent–progeny relationship (Nelson et al. 1977). Female American shad recruitment levels were regressed against May and June flow, water temperature, and rainfall data by a nonlinear multiple regression model:

$$\mathrm{Rp} = A \exp(d_1X_1 + d_2X_2 + \ldots . + d_nX_n)$$

where A = y-axis intercept, d_1 to d_n = exponent for each climatic factor, and X_1 to X_n = each climatic factor. The exponents (A, d_1–d_n) were estimated by nonlinear iteration (SAS 1982), and female American shad recruitment (Ra) was adjusted for average climatic conditions by multiplying the residuals (R/Rp) by the geometric mean recruitment value. These adjusted values were then refitted to the Ricker, Beverton–Holt, and Clark–Ricker models in order to reevaluate the statistical significance of the compensatory (b) and depensatory (c) mortality exponents.

All hydrographic and meteorological data used in this analysis were measured within the major spawning areas (river km 78–190) of American shad (Layzer 1974; Leggett 1976). Daily river flows (cubic metres per second) during May and June were recorded at Thompsonville, Connecticut (river km 89), by the U.S. Geological Survey, whereas daily water temperatures (degrees Celsius) were measured at the Holyoke Dam by the Holyoke Water Power Company. Total rainfall levels (millimetres) during May and June were recorded by the National Weather Service at Bradley Field Airport, Windsor Locks, Connecticut.

Environment-Dependent Stock–Recruitment Models

We developed nonlinear recruitment models for American shad, incorporating both density-dependent (female parent stock and the number of American shad lifted) and density-independent (river flow, temperature, rainfall) factors. The number of female American shad lifted (LF) annually over the Holyoke Dam (Table 1) was used as a predictor variable because the restoration of American shad to the Holyoke Dam impoundment is expected to enhance their reproductive success and recruitment in future years (Leggett 1977; Moffitt et al. 1982). The number lifted is a density-dependent factor, since it represents the fraction of the total parent stock that spawned in the Holyoke impoundment. Conversely, the fraction spawning below the Holyoke Dam (Pb) was expressed by $\mathrm{Pb} = P - \mathrm{LF}$, and the parent–progeny relationship was expressed by two density-dependent exponents: $R = AP \times \exp(b\mathrm{Pb} + c\mathrm{Lift})$. It is important to note that there was no significant serial correlation between Pb and LF ($r = 0.33$, $p < 0.4$) from 1966 to 1984.

A high degree of covariation among climatic variables would severely bias the parameter estimates of multiple regression models, reducing their overall precision and accuracy (Silvey 1969). The covariation among the climatic variables (June river flow, May and June rainfall, and June river temperature) was removed by replacing one of the original covariates (i.e., river temperatures) with adjusted temperatures (Table 1), defined as the geometric mean temperature from 1966–83 plus the residuals from the linear regression of June river flow and June temperature. This same method was also used to remove the covariation between May and June rainfall and June flow.

The stepwise multiple regression method (Draper and Smith 1981) was used to select the most significant ($p < 0.05$) climatic variables. The dependent-variable was the natural logarithm of recruitment divided by parent stock size ($\ln R/P$), thereby allowing the hydrographic and meteorological factors to exert a multiplicative effect on recruitment (Ricker 1975; Parrish and MacCall 1978). The linear form of all the multiple regression recruitment models:

$$\ln R/P = a + b\mathrm{Pb} + c\mathrm{Lift} + dX_1 + dX_2,$$

where a, b, c, d, and e, = estimates of the exponents and X_1 and X_2 = climatic factors, provided initial estimates of a, b, c, d, and e. The best least square estimates of the exponents and their asymptotic standard errors were determined by the nonlinear iterative method (SAS 1982). The use of nonlinear models was justified because the recruitment estimates from the linearized model ($\ln R/P$) are biased when back-transforming from the logarithmic to the arithmetic scale (Ricker 1975).

The best nonlinear models contained the lowest residual mean square (RMS) value and the highest coefficient of determination (r^2). We also plotted the residuals for each model against predicted recruitment (Rp) values and each explanatory variable (X). Recruitment models that exhibited serial correlations between the residuals and Rp, or with any of the explanatory variables (X), were deleted from further analysis.

Model Validation

The final step was to determine how well the models developed from the 1966–78 data could accurately forecast American shad recruitment from another data base. We used the most significant environment-dependent stock–recruitment models to predict the strength of the 1979–84 year-classes based on the juvenile indices of abundances for those years (Marcy 1976; Crecco et al. 1983). Because there was a significant positive correlation ($r = 0.90$, $p < 0.001$) between the juvenile indices from 1967–76 and the total number of virgin female American from these year-classes in the spawning runs (Crecco and Savoy 1985b), we assumed that the juvenile indices from

TABLE 2. Parent–progeny relationship for American shad based on Holyoke Lift data, 1966–78 (b = coefficient of density dependence; $*p < 0.05$).

Model	Equation	r^2	b	SE(b)	t
	Climatic effects included				
Ricker	$Rp = 3.00P \exp(-0.0033P)$	0.015	−0.0033	0.0022	1.50
Beverton–Holt	$Rp = P/0.003P + 0.0680$	0.010	0.0030	0.2020	0.01
Clark–Ricker	$Rp = 0.694P \exp(-0.005P) \exp(160.1/P)$	0.025	−0.0005	0.0032	0.16
	Climatic effects removed				
Ricker	$Ra = 4.76P \exp(-0.005P)$	0.259	−0.005	0.0007	7.14*
Beverton–Holt	$Ra = P/0.0037P - 0.084$	0.064	0.0037	0.0006	6.17*
Clark–Ricker	$Ra = 4.72P \exp(-0.005P) \exp(0.78/P)$	0.259	−0.005	0.0017	2.94*

TABLE 3. Nonlinear recruitment models without the density-dependent variable. JFW = mean June flow, MFW = mean May flow, and MJP = adjusted May–June rainfall

Model	r^2
$Rp = 417.57 \exp(-0.0026JFW) \exp(0.0030MJP)$	0.690
$Rp = 830.23 \exp(-0.0028JFW) \exp(0.0001MFW)$	0.631
$Rp = 835.43 \exp(-0.0029JFW)$	0.622

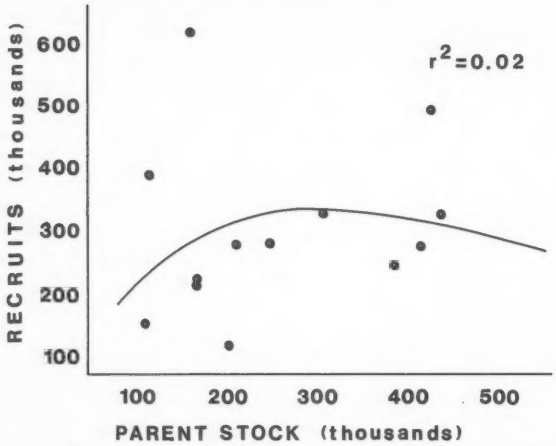


FIG. 1. Parent–progeny relationship for American shad based on the Holyoke recruitment data, 1966–78.

1979–84 accurately reflected the variability in year-class strength for those years. Each of the indices from 1979–84 was multiplied by 15 000 to scale them to the recruitment estimates from 1966–78 (Table 1). We predicted recruitment from 1979–84 by substituting the parent stock size and the key climatic variables into each model, from which the forecasting capability was evaluated by the magnitude of the r^2 value.

Results

Stock–Recruitment Analysis

The three stock–recruitment models explained less than 3.2% of the recruitment variation (Table 2), and the compensatory (b) and depensatory (c) density-dependent exponents

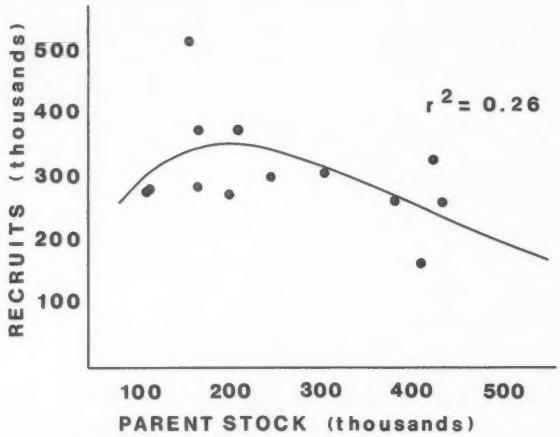


FIG. 2. Parent–progeny relationship when Holyoke recruitment was adjusted for May and June flows, 1966–78.

were not significant ($p < 0.05$). The very strong 1971 year-class and the very weak 1973 cohort were both produced by relatively small parent stocks, suggesting that year-class strength of American shad is independent of egg production over the range of female parent stocks observed from 1966–78 (Fig. 1).

Whereas recruitment variability of American shad was independent of parent stock size, it was strongly related to annual fluctuations in May and June river flows and total May and June precipitation (Table 3). The nonlinear environmental models accounted for over 63% of the recruitment variability, with over 60% of the variability being ascribed to annual fluctuations in June river flows. When recruitment variation attributed to May and June flows was removed, the adjusted recruitment levels were better described by the Ricker and Clark–Ricker models (Fig. 2), and the coefficients of density dependence (b) became highly significant. These data suggested that density-dependent processes are overshadowed by wide fluctuations in recruitment attributed to climatic factors. By contrast, the coefficient of depensatory mortality (c) in the Clark–Rickter model remained insignificant, indicating that this model was inappropriate for American shad. Because the r^2 value for the Ricker stock–recruitment model was higher than that for the Beverton–Holt, we selected the Ricker

TABLE 4. Stepwise multiple regression of log-transformed data ($\ln R/P$). P = parent stock, JFW = mean June flow, MFW = mean May flow, MJP = adjusted May–June rainfall, LF = female American shad lifted, and MSE = mean square error.

Data set	Number of variables	Explanatory variables	r^2	MSE
Holyoke lift	1	P	0.404	0.219
	2	P, JFW	0.870	0.052
	3	P, JFW, MFW	0.913	0.038
	4	P, JFW, MFW, LF	0.950	0.025

TABLE 5. Environment-dependent stock–recruitment models incorporating density-dependent and density-independent variables. JFW = mean June flow, MFW = mean May flow, MJP = adjusted May–June rainfall, LF = American shad lifted, P = parent stock size, SE = asymtotic standard error, and t = Student's t-statistic.

Parameters	SE	t	p
Model: $\mathrm{Rp} = 13.39P \exp(-0.0063P) \exp(-0.004\mathrm{JFW}) \times \exp(0.0007\mathrm{MFW}) \exp(0.0027\mathrm{LF})$			
$A = 13.39$	2.64	5.07	$p<0.001$
$P = -0.0063$	0.0006	10.5	$p<0.001$
JFW $= -0.004$	0.0005	8.0	$p<0.001$
MFW $= 0.0007$	0.0003	2.3	$p<0.05$
LF $= 0.0027$	0.0008	3.4	$p<0.001$
$r^2 = 0.913$			
Model: $\mathrm{Rp} = 16.66P \exp(-0.0057P) \exp(-0.0039\mathrm{JFW}) \times \exp(0.0004\mathrm{MFW})$			
$A = 16.66$	4.33	3.85	$p<0.001$
$P = -0.0057$	0.0008	7.13	$p<0.001$
JFW $= -0.0039$	0.0007	5.57	$p<0.001$
MFW $= 0.0004$	0.0002	2.00	$p<0.05$
$r^2 = 0.807$			
Model: $\mathrm{Rp} = 9.18P \exp(-0.0049P) \exp(-0.0033\mathrm{JFW}) \times \exp(0.002\mathrm{MJP})$			
$A = 9.18$	3.62	2.54	$p<0.02$
$P = -0.0049$	0.0005	9.8	$p<0.001$
JFW $= -0.0033$	0.0006	5.5	$p<0.001$
MJP $= 0.0025$	0.0012	2.1	$p<0.005$
$r^2 = 0.822$			

spawner–recruit model in developing the environment-dependent stock–recruitment models.

Environment-Dependent Stock–Recruitment Models

The stepwise regression procedure selected parent stock as the most significant single-variable model. However, its r^2 of 0.40 is biased upward because P appears on both sides of the linearized equation: $\ln(R/P) = a + bP$. Mean June flow was chosen as the most significant hydrographic variable with parent stock size in the log-transformed models (Table 4), explaining over 84% of the recruitment variability. The best three-variable models included June flow, parent stock size, and mean May flow. When these models were refitted by the nonlinear regression method, they explained over 80% of the recruitment variability (Table 5). The number of female American shad lifted into the Holyoke impoundment (LF) was selected as a fourth significant predictor variable with June flow, parent stock size, and May flow. It explained over 90% of the variability in American shad recruitment from 1966–78 when this model was fitted by the nonlinear regression method (Fig. 3).

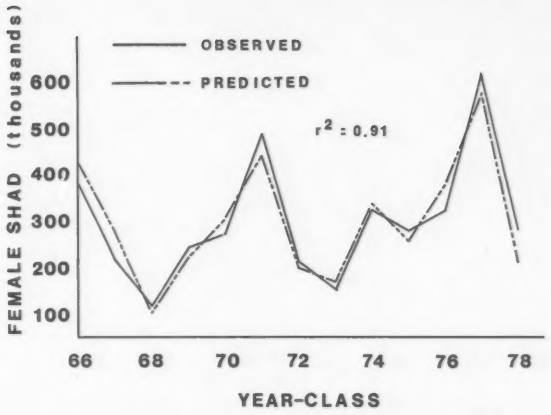


FIG. 3. Relationship between the observed and predicted Holyoke recruitment estimates based on the nonlinear model containing below Holyoke parent stock (Pb), above Holyoke parent stock (LF), mean June flows, and mean May flows.

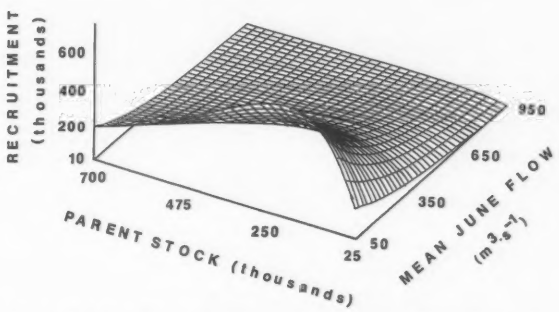


FIG. 4. Relationship of American shad recruitment (R) to changes in parent stock size and mean June flows with May–June rainfall held constant (203 mm).

Density-Dependent and Density-Independent Effects

The three-variable model, containing parent stock size, June flow, and adjusted May–June rainfall, was used to examine how recruitment varied when June flow and parent stock size varied together, holding May–June rainfall constant (203 mm) at the mean level from 1966–78. The three-dimensional recruitment curve (Fig. 4) showed that low (50–100 $m^3 \cdot s^{-1}$) June flows produced strong year-classes of American shad at moderate parent stock levels (150 000 to 300 000 spawners), but not at high levels (500 000 to 700 000 spawners) due to the greater influence of density-dependent mortality. When the parent stock drops to low levels (10 000 to 50 000 spawners), low June flows were less effective in producing strong year-classes because the spawning stock approached the limits of its compensatory reserve. Conversely, high June flows (600–800 $m^3 \cdot s^{-1}$) caused the production of poor year-classes of

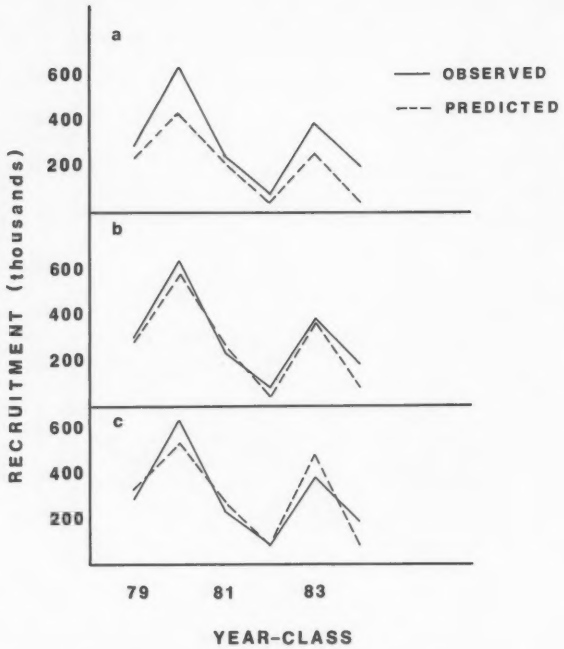


FIG. 5. Observed and predicted recruitment estimates from 1979–84 based on three environment-dependent stock–recruitment models:

(a) $R = 16.66P \exp(-0.0057P) \exp(-0.0039\text{JFW}) \times \exp(0.0004\text{MFW})$

(b) $R = 13.39P \exp(-0.0063P) \exp(-0.004\text{JFW}) \times \exp(0.0007\text{MFW}) \exp(0.0027\text{LF})$

(c) $R = 9.18P \exp(-0.0049P) \exp(-0.0033\text{JFW}) \times \exp(0.0025\text{MJP})$.

American shad regardless of parent stock size, indicating that major climatic events overshadow the compensatory mechanism of the population.

Model Validation

The environment-dependent stock–recruitment models with either parent stock, June flow, and adjusted May–June rainfall or parent stock below Holyoke, American shad lifted, June flow, and May flow explained 80.5 and 88.9%, respectively, of the recruitment variability from 1979–84 (Fig. 5). The model with parent stock, June flow, and May flow accounted for only 55.2%. This analysis indicated that two of the three models accurately predicted year-class strength from a different data base.

Discussion

The method of combining environment factors, having known biological effects on recruitment (Austin and Ingham 1978; Parrish and MacCall 1978), with stock–recruitment data provides a unifying approach to better understanding the various pathways through which climatic and density-dependent factors affect recruitment. This approach is superior to applying regression methods to recruitment and lagged environmental data in the hope of discovering significant statistical fits. Many correlation studies have failed (Walford 1946; Carruthers et al. 1951; Sissenwine 1974; Summers et al. 1982) to demonstrate which life stages are affected, the proper spatial and temporal scale for each climatic event, and whether these variables represent the proximal or ultimate determinant of year-class strength (Parrish et al. 1981). As a result, the causal mechanisms from these studies are often vague or left unspecified. Another advantage of the environment-dependent stock–recruitment models is their ability to accurately forecast year-class strength during prerecruitment so that management regulations can be imposed on a timely basis. With this information it is practical to increase the harvest rate on strong year-classes, while avoiding excessive exploitation of poor year-classes.

The relative importance of parent stock size (density-dependent factors) and environmental factors on American shad recruitment is demonstrated by our environment-dependent stock–recruitment models. Not only were the density-dependent terms (b) in all the models statistically significant (Table 5), but the inclusion of parent stock size explained significantly more (15–20%) of the recruitment variability than models containing only environmental variables (Table 3). These findings support our conclusions that density-dependent regulations exert a subtle but measurable influence on year-class recruitment of American shad in the presence of climatic variability.

The negative exponents for June river flow, the most significant hydrographic variable, support our working hypothesis that high and turbulent June flow rates promote unfavorable feeding conditions for first-feeding larvae (Crecco et al. 1983; Crecco and Savoy 1984), reducing larval survival and, ultimately, year-class strength. The positive exponents for May flow and total May–June rainfall in the presence of June river flow were unexpected and difficult to explain. The most reasonable explanation is that high May rainfall and flow depress May water temperatures, thereby postponing the onset of American shad spawning (Leggett and Whitney 1972) and larval hatching (Cave 1978) until mid-June, during which low flows produce optimal conditions for the high feeding success and survival of American shad larvae (Crecco et al. 1983; Crecco and Savoy 1984). Lastly, the significant density-dependent exponent for the number of American shad lifted is consistent with the hypothesis that the restoration of adult American shad to additional spawning areas has improved reproductive success and subsequent recruitment (Moffitt et al. 1982).

Acknowledgments

We thank Ernesto Lorda, David Witherall, Deborah Pacileo, and Rita Lorenzetti-Langan for their help in the field and laboratory. We also thank the two anonymous reviewers for their comments on an earlier version of the manuscript.

References

AUSTIN, H. M., AND M. C. INGHAM. 1978. Use of environmental data in the prediction of marine fisheries abundance, p. 93–108. *In* Climate and fisheries. The Center for Ocean Management Studies, University of Rhode Island, Kingston, RI.

BELSLEY, D. A., E. KUH, AND R. E. WELSCH. 1980. Regression diagnostics: identifying influence data and sources of collinearity. John Wiley & Sons, New York, NY 292 p.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish. Fish. Invest. (Ser. 2) 19: 533.

CAVE, J. R. 1978. American shad, *Alosa sapidissima*, larval distribution, relative abundance and movement in the Holyoke Pool, Connecticut River, Massachusetts. Masters thesis, University of Massachusetts, Amherst, MA. 65 p.

CARRUTHERS, J. N., A. L. LAWFORD, V. P. C. VELEY, AND B. B. PARISH. 1951. Variations in brood-strength in the North Sea haddock in the light of relevant wind conditions. Nature (Lond.) 168: 317–319.

CLARK, C. W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. Int. Explor. Mer 36: 7–14.

CRAIG, R. E. 1960. A note on the dependence of catches on temperature and wind in the Bushan prespawning herring fishery. J. Cons. Int. Explor. Mer 25(2): 185–190.

CRECCO, V. A. 1985. Effects of hydrographic fluctuations on year-class strength of Connecticut River shad, *Alosa sapidissima*. Ph.D. thesis, University of Connecticut, Storrs, CT. 74 p.

CRECCO, V. A., L. GUNN, AND T. SAVOY. 1981. The Connecticut River shad study, 1980 final report. Connecticut Department of Environmental protection, AFC 12: 136 p.

1982. The Connecticut River shad study, 1981. A progress report. Connecticut Department of Environmental Protection, AFC 13: 61 p.

CRECCO, V. A., AND T. F. SAVOY. 1984. Effect of fluctuations in hydrographic conditions on year-class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Can. J. Fish. Aquat. Sci. 41: 1216–1223.

1985a. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42: 1640–1648.

1985b. Density-dependent catchability and its potential causes and consequences on Connecticut River American shad, *Alosa sapidissima*. Can. J. Fish. Aquat. Sci. 42: 1649–1657.

CRECCO, V., T. SAVOY, AND L. GUNN. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Can. J. Fish. Aquat. Sci. 40: 1719–1728.

1984. Population dynamics studies of American shad in the Connecticut River. Final Report. Department of Environmental Protection, AFC 13: 75 p.

CUSHING, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, NY. 278 p.

1982. Climate and fisheries. Academic Press, New York, NY. 373 p.

DRAPER, N., AND H. SMITH. 1981. Applied regression analysis. John Wiley & Sons, New York, NY. 709 p.

GULLAND, J. A. 1977. The stability of fish stocks. J. Cons. Int. Explor. Mer 37(3): 199–204.

JONES, R. A., P. MINTA, AND V. A. CRECCO. 1976. A review of American shad studies in the Connecticut River, p. 135–164. *In* Proceedings of a Workshop on American Shad. U.S. National Marine Fisheries Service, Amherst, MA.

LAYZER, J. B. 1974. Spawning sites and behavior of American shad, *Alosa sapidissima*, (Wilson), in the Connecticut River between Holyoke and Turners Falls, Massachusetts, 1972. Masters thesis, University of Massachusetts, Amherst, MA 46 p.

LEGGETT, W. C. 1976. The American shad (*Alosa sapidissima*), with special reference to its migrations and population dynamics in the Connecticut River, p. 169–225. *In* D. Merriman and L. M. Thorpe [ed.] The Connecticut River ecological study: the impact of a nuclear power plant. Am. Fish. Soc. Monogr. I: 252 p.

1977. Density dependence, density independence and recruitment in the American shad (*Alosa sapidissima*) population of the Connecticut River, p. 3–17. *In* Oak Ridge Natl. Lab. Energy Res. Dev. Adm. and Electric Power Res. Inst. Proceedings of the Conference on Assessing the Effects of Power-Plant Induced Mortality on Fish Populations. 380 p.

LEGGETT, W. C., AND R. R. WHITNEY. 1972. Water temperature and the migrations of American shad. Fish. Bull. U.S. 70(3): 659–670.

MARCY, B. C. JR. 1976. Early life history studies of American shad in the lower Connecticut River and the effects of the Connecticut Yankee Plant, p. 141–168. *In* D. Merriman and L. M. Thorpe [ed.] The Conecticut River ecological study: the impact of a nuclear power plant. Am. Fish. Soc. Monogr. I: 252 p.

MOFFITT, C. M., B. KYNARD, AND S. G. RIDEOUT. 1982. Fish passage facilities and anadromous fish restoration in the Connecticut River. Fisheries 7: 2–11.

NELSON, W., M. INGHAM, AND W. SCHAEF. 1977. Larval transport and year class strength of Atlantic menhaden, *Brevoortia tryannus*. Fish. Bull. U.S. 75: 23–41.

PARRISH, R. H., AND A. D. MACCALL. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish. Game Fish. Bull. 167: 110.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1(2): 175–203.

PETERMAN, R. M., W. C. CLARK, AND C. S. HOLLING. 1979. The dynamics of resilience: shifting stability domains in fish and insect systems. *In* R. M. Anderson, B. Turner, and R. E. Taylor [ed.] Population dynamics. Blackwell Scientific Publications, Oxford.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board. Can. 11: 559–586; 609–623.

1975. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 382 p.

SAS. 1982. Statistical analysis system user guide. SAS Institute, Inc., Cary, NC. 584 p.

SHEPARD, J. G. 1982. A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yields curves. J. Cons. Int. Explor. Mer 40(1): 67–75.

SILVEY, S. D. 1969. Multicollinearity and imprecise estimation. J. R. Stat. Soc. Ser. B(31): 539–552.

SINCLAIR, M., A. SINCLAIR, AND T. D. ILES. 1982. Growth and maturation of southwest Nova Scotia Atlantic herring (*Clupea harengus harengus*). Can. J. Fish. Aquat. Sci. 39: 288–295.

SISSENWINE, M. P. 1974. Variability in recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery. J. Cons. Int. Explor. Mer 36(1): 15–26.

STOCKER, M., V. HAIST, AND D. FOURNIER. 1985. Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 174–180.

SUMMERS, J. K., W. A. RICHKUS, R. N. ROSS, AND R. E. ULANOWICZ. 1982. A statistical model of white perch (*Morone americanus*) harvest assessment in relation to environmental variation. Fish. Res. 1: 289–298.

SUTCLIFFE, W. H. JR., K. DRINKWATER, AND B. S. MUIR. 1977. Correlation of fish catch and environmental factors in the Gulf of Maine. J. Fish. Res. Board Can. 34: 19–30.

WALFORD, L. A. 1946. Correlation between fluctuations in abundance of the Pacific sardine (*Sardinops caerulea*) and salinity of the sea water. J. Mar. Res. 6(1): 48–53.

YOSHIYAMA, R. M., W. VANWINKLE, B. L. KIRK, AND D. E. STEVENS. 1981. Regression analyses of stock–recruitment relationships in three fish populations. Res. Rep. W-7405-eng-26. Nuclear Regulatory Research, Oak Ridge National Laboratory, Oak Ridge, TN.

REVIEWS/SYNTHÈSES

El Niño, Interannual Variability and Fisheries in the Northeast Pacific Ocean

Lawrence A. Mysak[1]

Departments of Mathematics and Oceanography, The University of British Columbia, Vancouver, B.C. V6T 1Y4

Mysak, L. A. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43: 464–497.

In this review I describe the oceanic and atmospheric observations, physical mechanisms, and theories associated with El Niño – Southern Oscillation (ENSO) warming episodes in the tropical Pacific, and critically examine the means by which these anomalous events are believed to produce unusual conditions in the northeast Pacific. However, not all tropical ENSO episodes have a noticeable effect at higher latitudes. Also, because of anomalous local atmospheric forcing, significant warmings, strong coastal currents, and high sea levels along the west coast of North America can occur in years during which there are no tropical ENSO episodes. The possible impacts of ENSO-induced changes and of other interannual fluctuations in the northeast Pacific on various fisheries are described. Such impacts include changes in the migration routes of the bluefin tuna (*Thunnus thynuus*) and Fraser River sockeye salmon (*Oncorhynchus nerka*), increases in the Pacific herring (*Clupea pallasi*) recruitment, earlier return times for the Bristol Bay sockeye salmon, and increases in the weight of mature Fraser River sockeye several years after a local warming event.

Dans la présente étude, je décris les observations réalisées dans l'océan et dans l'atmosphère, les mécanismes physiques et les théories qui sont associés aux périodes de réchauffement dues à l'oscillation méridionale El Niño (OMEN) dans la partie tropicale du Pacifique, et j'examine d'un oeil critique les hypothèses visant à expliquer de quelle façon ces anomalies sont à l'origine des conditions inhabituelles observées dans le nord-est du Pacifique. Cependant, ce ne sont pas toutes les épisodes d'OMEN dans les tropiques qui ont un effet perceptible à des latitudes plus élevées. En outre, une pression atmosphérique locale anormale peut entraîner des réchauffements importants, de puissants courants côtiers et des niveaux d'eau élevés le long de la côte ouest de l'Amérique du Nord les années où il n'y a pas de périodes d'OMEN dans les tropiques. On décrit les répercussions que peuvent avoir sur diverses pêches les changements provoqués par l'OMEN et d'autres variations qui se produisent d'une année à l'autre dans le nord-est du Pacifique. Ces répercussions comprennent, entre autres, des changements dans les routes de migration du thon rouge (*Thunnus thynnus*) et du saumon rouge (*Oncorhynchus nerka*) du fleuve Fraser, une augmentation du recrutement de harengs du Pacifique (*Clupea pallasi*), un retour plus hâtif des saumons rouges de la baie Bristol et un accroissement du poids des saumons rouges adultes du fleuve Fraser plusieurs années après qu'il y ait eu réchauffement au niveau local.

Received November 26, 1984
Accepted October 2, 1985
(J8026)

Reçu le 26 novembre 1984
Accepté le 2 octobre 1985

Several recent books deal with the influence of climatic changes on fisheries (e.g. Cushing 1982; Wooster 1983a; McCleave et al. 1984; Pearcy 1984). However, there is relatively little discussion of what is agreed (U.S. Climate Research Committee 1983) to be the largest interannual climatic fluctuation in the atmosphere–ocean system: the Southern Oscillation over the tropical South Pacific Ocean and the closely connected El Niño phenomenon, jointly referred to here as ENSO. The Southern Oscillation (SO) is manifested as a seesaw variation in the atmospheric pressure difference between the southeast Pacific subtropical high and the Australian–Indonesian low. The oscillation period, though irregular, lies in the range of 2–7 yr. El Niño refers to a large-scale anomalous warming of the tropical Pacific Ocean, which at its peak can extend from the west coast of South America to the dateline. Such an elongated pool of warm water straddling the equator may persist for two or more seasons (as in 1982–83), but this anomaly occurs only every few years, generally shortly after a shift of atmospheric mass from Indonesia to the western Pacific (which is part of the SO).

My objectives in this review are (i) to describe the physical processes in the ocean and atmosphere associated with this strong, climatic fluctuation; (ii) to discuss the mechanisms by which this tropical phenomenon can produce interannual changes in the atmospheric and oceanic conditions in the northeast Pacific; and (iii) to indicate how these and other observed interannual variations in the northeast Pacific may affect the regional fisheries (abundance and migration).

According to Wooster (1983b), environmental changes are

[1]Also member, Institute of Applied Mathematics, University of British Columbia.

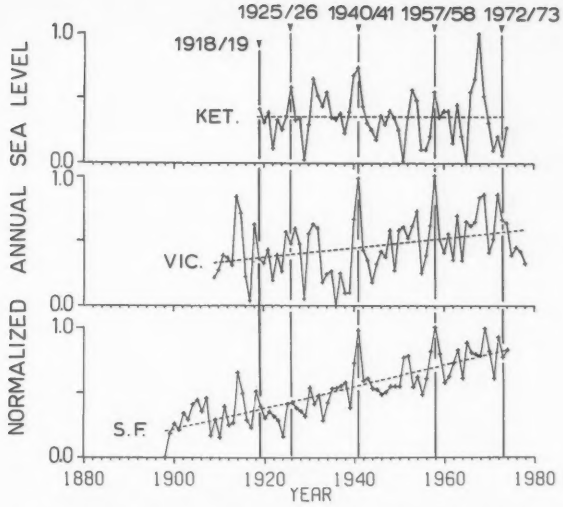


FIG. 1. Annual sea level time series for Ketchikan (in southeastern Alaska), Victoria, and San Francisco (from Mysak et al. 1982, hereafter referred to as MHP). Each series x has been normalized to lie between 0 and 1 by plotting $(x - m)/(M - m)$, where M and m are the maximum and minimum values of x. In the case of Ketchikan, M = 50.9 cm and m = 32.3 cm, for example. (See table 2 in MHP for the remaining values of M and m.) The arrowheads at top and corresponding vertical lines denote major ENSO events lasting 1 yr or longer, viz. 1918–19, 1925–26, 1940–41, 1957–58, and 1972–73. The approximately horizontal broken lines indicate the trends found by polynominal least squares fitting.

likely to produce a significant portion of the observed interannual variability in fish populations. As evidence of this, Soutar and Isaacs (1974) have shown that long before commercial fisheries were established, certain United States west coast species exhibited marked fluctuations in stock abundance. More recently, several investigators have found strong correlations between fluctuations in environmental physical variables and in various fish stocks. However, to determine whether a cause-and-effect relationship exists, plausible hypotheses have to be tested using field and laboratory data. For this purpose, it is necessary to have a thorough understanding of the mechanisms and processes involved in the observed environmental variability. It is my belief that we are now arriving at a sufficient understanding of physical environmental changes (such as ENSO) which will enable us to do better than simply treat them as "random noise" in fish population and stock–recruitment models (Shepherd and Horwood 1979; Ludwig and Walters 1982).

Mysak et al. (1982; hereafter referred to as MHP) have shown that a 5–6 yr cycle in British Columbia coastal sea level, sea surface temperature, and salinity fluctuations is highly coherent with the regional herring recruitment and annual sockeye salmon (*Oncorhynchus nerka*) catch. MHP speculated that the oceanic signal may be driven by the SO, but the connection with El Niño was overlooked. With the recent 1982–83 ENSO event, I was stimulated to reexamine the oceanic and fisheries time series analyzed by MHP. Large peaks (or anomalies) in both the physical and fisheries time series indeed occurred in several ENSO years (e.g. 1925–26, 1940–41, and 1957–58). Moreover, during the past 40 yr,

TABLE 1. Catalogue of independent twentieth century ENSO (warming) events according to Quinn et al. (1978). For the period 1763–1972, the average interval between strong events is 12.3 yr; for the period 1791–1976, the average interval between strong and moderate events is 5.4 yr (Quinn et al. 1978). Most events have their onset off the Ecuador–Peru coast in January of the year listed (first year for the case of strong events) and last from several months to over 1 yr. However, the strong events of 1940–41 and 1982–83 had their onset in the middle of the first year given.

Strong	Moderate	Weak
1899–1900		
	1902	
	1905	
1911–12		
	1914	
		1917
1918–19		
		1923
1925–26		
	1929–30	
		1932
	1939	
1940–41		
		1943
		1951
	1953	
1957–58		
		1963[a]
	1965	
		1969
1972–73		
	1976	
1982–83[b]		

[a]According to Rasmusson and Carpenter (1982), but quite weak.
[b]The most recent ENSO event (Cane 1983; Gill and Rasmusson 1983).

eight ENSO events have been recorded (Rasmusson and Carpenter 1982); this gives an average period of 5 yr for the ENSO signal, which is very close to the 5–6 yr signal detected by MHP. However, because ENSO events do not appear at regular intervals, the spectral analysis techniques used by MHP may not be the most appropriate way to study time-varying fish–environment interactions. Now I recommend an event-by-event analysis of the data as well as simple lag-correlation calculations.

Interannual Variability in the North Pacific

Sea Level

Interannual fluctuations in the California coast sea level were noted some time ago (e.g. Roden 1966), but it is only recently that these anomalies have been analyzed with a view toward determining the presence of large-scale patterns and the connections with ENSO events. Figure 1 shows the normalized time series of annual mean sea level from three coastal stations which span a total distance of 2000 km. The records contain many large peaks in common, several of which coincide with major ENSO events in the tropical Pacific. According to Quinn et al. (1978), strong ENSO events in this century occurred during 1911–12, 1918–19, 1925–26, 1940–41, 1957–58, 1972–73, and 1982–83. Several moderate and weak ENSO events took place during the intervening years (see Table 1),

but these are not generally visible as a strong signal in the time series records from midlatitudes. Also, not even all strong (tropical) ENSO events are accompanied by anomalously high sea levels at midlatitudes (e.g. see the 1972–73 event marked in Fig. 1). The recent 1982–83 ENSO episode is regarded as the strongest in this century (Cane 1983; Gill and Rasmusson 1983; Rasmusson and Wallace 1983), and it resulted in the highest sea levels ever being recorded during winter and spring 1983 along the California (Simpson 1983) and British Columbia (Tabata 1984a) coasts.

From a cross-spectral analysis of the monthly sea level fluctuations from San Francisco and Victoria, MHP found a broadband 5–6 yr period signal which travelled northward at a phase speed of 36 km·d^{-1} (0.42 m·s^{-1}). Thomson and Tabata (1981), on the other hand, detected a 5.7 yr sea level signal which travelled northward along the California – British Columbia coast with a phase speed of 25–30 km·d^{-1}. Enfield and Allen (1980) and Chelton and Davis (1982) showed that such northward-travelling sea level disturbances extend all the way from the tropics to Alaska; they estimated the average propagation speed to be 75 and 35 km·d^{-1}, respectively. In the past, such signals have often been interpreted as first vertical-mode baroclinic (internal) Kelvin waves which are trapped against the coast (LeBlond and Mysak 1978, Chap. 4). In the Northern (Southern) Hemisphere the crests of such waves, which produce 180° out-of-phase sea level and thermocline displacements (see Fig. 2), travel with the coast to the right (left) of the direction of phase propagation. Hence, the observed northward propagation of sea level fluctuations along the west coast of North America is consistent with such a wave motion. However, the thoretical phase speed, c, for a freely propagating first-mode internal Kelvin wave is about two to three times larger than the observed range of speeds. For the two-layer ocean model illustrated in Fig. 2 (in which the interface represents the thermocline, the upper layer models the relatively thin, warm mixed layer, and the lower layer approximates the deep cold abyssal region), $c \simeq \sqrt{g'h_1} = 1.41$ m·s^{-1} (122 km·d^{-1}) for $g' = 2 \times 10^{-2}$ m·s^{-2} and $h_1 = 100$ m (typical west coast values) (see Fig. 2 caption for definitions of g' and h_1 and derivation of c). A second difficulty with the Kelvin wave interpretation is that if it is propagating as a free sinusoidal wave with a period of, say, 5 yr, then its wavelength, L, is much longer than the circumference of the North Pacific Ocean: $L = cT = 65\,700$ km for the MHP observed values of $c = 36$ km·d^{-1} and period $T = 5$ yr. A more realistic interpretation of the northward-travelling signal may be to think of it as a wave front or pulse (as shown in Fig. 2) which is generated at irregular intervals (by ENSO events) in the eastern equatorial Pacific (Hurlburt et al. 1976; McCreary 1976).

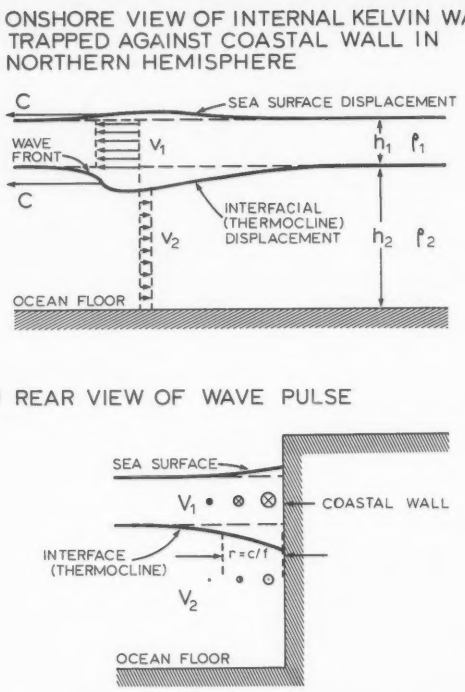


FIG. 2. Schematic view of a Northern Hemisphere internal Kelvin wave pulse in a two-layer ocean, looking (a) toward the coast and (b) from behind the wave pulse. The two-layer ocean shown here is the simplist model that can be used to approximate the first vertical mode in the real ocean in which the density varies continuously with depth. The quantities v_i, h_i, and ρ_i denote, respectively, the longshore current, mean depth, and density in layer i ($i = 1,2$). The wave front and sea level displacement both travel with phase speed $c = (g'h_1h_2/h)^{1/2}$, where $g' = g(\rho_2 - \rho_1)/\rho_1$ is the reduced gravity, g is the gravitational acceleration, and $h = h_1 + h_2$ is the total depth (LeBlond and Mysak 1978, Chap. 4). Generally, $|v_1| \ll c$, so that the wave front (thermocline depression) travels much faster than the longshore current in the upper layer. For an internal Kelvin wave in a two-layer ocean, $h_1v_1 + h_2v_2 = 0$, i.e. the vertically integrated horizontal mass transport is zero. Thus, at any time instant, v_1 and v_2 flow in opposite directions. Since $h_1 \ll h_2$ in the ocean, this relation implies that $|v_1| \gg |v_2|$ and that the phase speed can be approximated by $c \simeq (g'h_1)^{1/2}$. Away from the coast the wave amplitude and current decay exponentially, in the manner $e^{-x/r}$, where x is the offshore distance and $r = c/f$ is the internal Rossby radius of deformation. In the latter expression, $f = 2\Omega\sin\theta$ is the Coriolis parameter, where θ is the latitude and Ω is the earth's angular velocity ($\Omega = 0.73 \times 10^{-4}$ s^{-1}).

Sea Surface Temperature and Salinity

Roden (1958) found that time series of sea surface temperature (SST) and salinity from stations along the west coast of North America also exhibit marked interannual fluctuations. Some of the anomalies (peaks) in these series are closely correlated with ENSO events. Figures 3 (top) and 4 show, for example, that during the strong 1957–58 ENSO event, a significant warming extended from the equator to the British Columbia – Alaska coast. Coastal salinity, however, tended to be anomalously low during these years (see Fig. 3, bottom). During the recent 1982–83 event, the SST off the British Columbia coast was also anomalously high (Freeland and Giovando 1984). However, during the preceding strong ENSO event (1972–73), the British Columbia coastal SST records show that no significant warming occurred (Fig. 3).

Recent studies of British Columbia coastal SST anomalies have been carried out by Thomson et al. (1984) and by Emery and Hamilton (1985), who noted that local warming events can also occur in years when there are no strong ENSO events (e.g. 1963 and 1981). Examples of interannual variability of offshore SST's in the North Pacific are given in Favorite and McLain (1973), Davis (1976), Haney (1980), and Reynolds and Rasmusson (1983). The year-to-year changes in the sub-

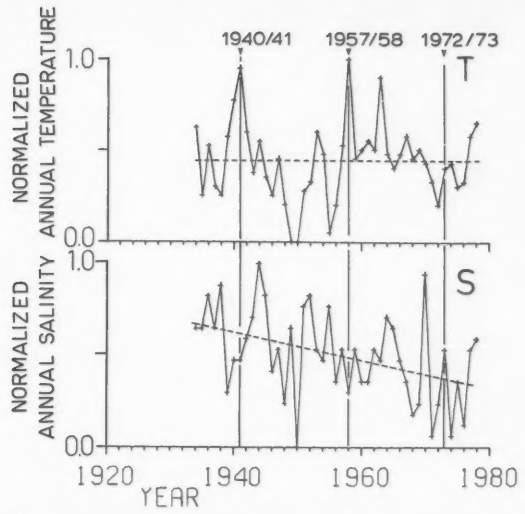


FIG. 3. Normalized annual temperature (T) and salinity (S) at Amphitrite Point, west side of Vancouver Island (see Fig. 18c below (from MHP)). Major ENSO events are marked by arrowheads and vertical lines.

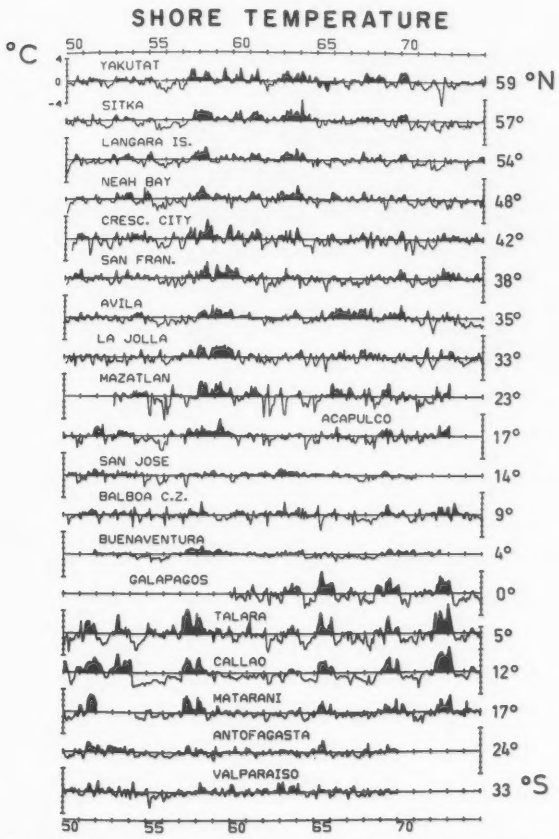


FIG. 4. Time series of monthly anomalies of shore temperature along the west coasts of South and North America (from Enfield and Allen 1980). The approximate latitude of each station is given on the right.

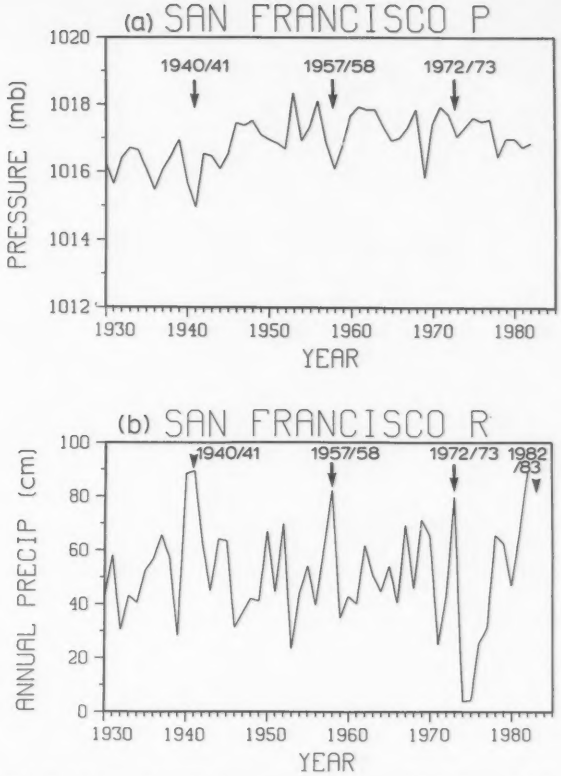


FIG. 5. (a) Annual sea level atmospheric pressure P and (b) rainfall R at San Francisco (courtesy of K. P. Hamilton, McGill University, Montreal, Que.). Major ENSO events are indicated by arrows at top.

surface temperature and salinity along Line P and at Station P have been described by Tabata (1981).

Atmospheric Pressure and Rainfall

Interannual fluctuations in the atmospheric pressure, rainfall, and air temperature in the North Pacific and their relationship with ENSO events have been studied by Horel and Wallace (1981), van Loon and Madden (1981), and Rasmusson and Wallace (1983). Figure 5 shows the sea level atmospheric pressure and rainfall at San Francisco during the period 1930–82. The anomalously low pressure during the 1940–41 and 1957–58 ENSO events (Fig. 5a) can partly account, through the inverse barometer effect, for the anomalously high sea level observed at San Francisco during those years (see Fig. 1). Figure 5b shows that the annual rainfall during the major ENSO years 1940–41, 1957–58, and 1972–73 was approximately twice the climatological mean for the past 50 yr. The steep rise shown in 1981 and 1982 culminated in a 1983 California rainfall which was about three times the climatological mean.

Fisheries Data

Examples of interannual fluctuations of nonsalmonid fish stock abundance are given in Wooster (1983a). Year-to-year changes in Oregon Dungeness crab (*Cancer magister*) catches

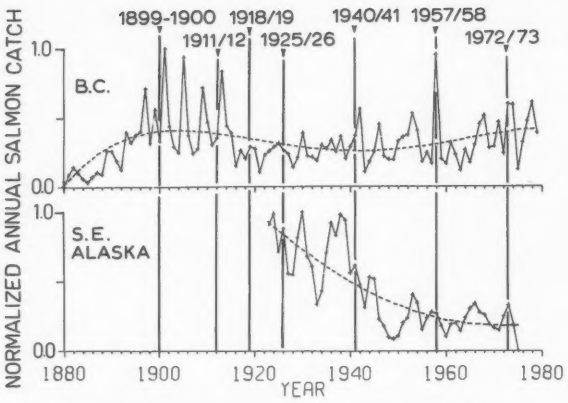


FIG. 6. Normalized annual sockeye salmon catches in British Columbia and southeastern Alaska (from MHP). Major ENSO events are marked by arrowheads and vertical lines.

have been noted by Peterson and Smith (1979), and interannual fluctuations in zooplankton abundance off California have been described by Bakun and Parrish (1980) and Chelton et al. (1982). Figure 6 shows the time series of the annual sockeye salmon catches in British Columbia and southeastern Alaska. The 4-yr signal seen during the period 1897–1913 in the top part of Fig. 6 is mostly due to the strong "1901 run" of the Fraser River sockeye, which during this period dominated the British Columbia catch. The 4-yr periodicity occurs because the Fraser River sockeye are mostly a 4-yr fish, from egg to returning spawner. However, during winter of 1912–13, a large amount of rock from the construction of the Canadian National Railways fell into the Fraser River near Hell's Gate Canyon. As a consequence, few of the returning spawners passed upstream in the summer of 1913 and the fabulous 1913 run has never recovered; also, the subsequent interannual variability shows no clear 4-yr signal (i.e. no domination by any particular run). However, during or shortly after the major ENSO events of 1918–19, 1925–26, 1940–41, 1957–58, and 1972–73 (see Fig. 6), the British Columbia sockeye catch shows a local maximum. Hence, major ENSO events, which can induce changes in the ocean conditions in the northeast Pacific, may be partly responsible for these anomalous catches. The southeastern Alaska catch, however, is only marginally correlated with major ENSO events.

Seasonal tropical El Niño, Its Occasional Amplification, and the Southern Oscillation

Seasonal El Niño

The term El Niño ("the child" in Spanish) originally referred to the annual appearance around Christmas of a warm southward-flowing current off Ecuador and Peru which generally comes at the end of the local fishing season during which upwelling is prevalent. The El Niño coastal current and associated warm shore temperatures normally persist for about 3 mo (until the end of March); then there is a rapid return to cool water conditions in April–May (see the Talara temperature anomalies during the "normal" non-ENSO years 1962, 1964, 1966, 1967, 1968, and 1970 in Fig. 7).

Since the local winds are also favorable for upwelling during the seasonal El Niño (Enfield 1981; Smith 1983), it remained a mystery as to what produced the warm coastal water. According to Busalacchi and O'Brien (1981), the local warming could be caused by changes in the easterly trade winds in the central equatorial Pacific (between 120 and 180°W). During the northern fall, the trades there tend to relax, and each such relaxation event generates a downwelling equatorial internal Kelvin wave pulse which travels eastward along the thermocline toward the coast of South America at a phase speed of about 2.5 $m \cdot s^{-1}$ (216 $km \cdot d^{-1}$). In a two-layer ocean, the horizontal current pattern and thermocline displacement of an equatorial internal Kelvin wave pulse is trapped along an equatorial wave guide (see Fig. 12). A downwelling Kelvin wave generated near the dateline (180°W) in November, say, will reach the Ecuador coast (at 80°W) about 2 mo later, during the El Niño season. The effects will be a depressed thermocline and higher sea levels at the coast. Local solar heating (Weare 1983) and wind mixing will then warm up coastal waters down to a depth of 100 m or more. Consequently, upwelling-favorable winds during El Niño can only bring up warm subsurface water.

Amplified El Niño

Figure 7 shows that during the years 1963, 1965, and 1969 the warming of the coastal water lasted more than one season, with temperatures rising to about 4°C above the 10-yr mean. Recently, the term El Niño has been used for such amplified warming events which have their onset in January. Associated with these anomalous warmings are increased rainfall in Ecuador and Peru, and a crippling of the local economy due to widespread mortality of fish and guano birds. In 1982 the SCOR (Scientific Committee for Oceanic Research) Working Group 55 agreed to officially define El Niño as "The appearance of anomalously warm water along the coast of Ecuador and Peru as far south as Lima (12°S) during which a normalized SST anomaly exceeded one standard derivation (typically 1.5–2° C) for at least four consecutive months at three or more of five coastal stations extending from Talara to Lima, Peru." It is now recognized that the anomalous warm coastal water can extend much farther offshore. Rasmusson and Carpenter (1982) recently produced composite plots of SST anomalies for the whole tropical Pacific by averaging data for six El Niño events which occurred between 1950 and 1973. Following the coastal warming which lasts until May (Fig. 8a), the warm water spreads westward toward the dateline (Fig. 8b), resulting in a large warm pool having an east–west extent of about 10 000 km (Fig. 8c). The persistence of SST anomalies in the tropical Pacific for several seasons was recognized by Bjerknes (1966, 1969, 1972) and others as a possible heat source for the generation of long-period (interannual) fluctuations in the atmosphere, such as the SO.

Southern Oscillation

In his study of interannual atmospheric fluctuations in the Southern Hemisphere, Sir Gilbert Walker observed the "swaying of pressure on a big scale backwards and forwards between the Indian and Pacific Oceans," a phenomenon now known as the Southern Oscillation (SO) (see Horel and Wallace (1981) and the review by Wright (1985)). In the SO, the sea level pressure anomalies in the Australian–Indonesian low-pressure zone tend to be of opposite sign to those in the South Pacific high-pressure zone. Thus, the pressure difference between these two regions exhibits an oscillatory behavior, as

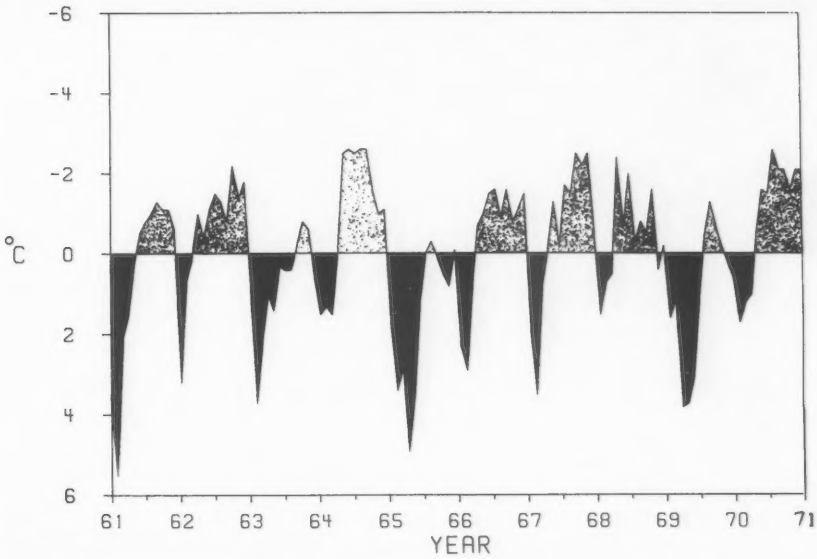


FIG. 7. Time series of monthly anomalies of shore temperatures at Talara, Peru (4.6°S, 81.2°W), from January 1961 to December 1970 (from Busalacchi and O'Brien 1981).

seen in Fig. 9a. However, the oscillation period (time interval between successive peaks in the heavy curve in Fig. 9a) is irregular, and ranges from 2 to 7 yr (Trenberth 1976; Wright 1985). A smoothed version of this signal is called the Southern Oscillation Index (SOI) (Fig. 9b). The shading in Fig. 9b indicates the Horel and Wallace (1981) definition of major warm SST episodes in the central equatorial Pacific region bounded by 5°N–5°S and 180–140°W. There is nearly a one-to-one correspondence between the warm episodes defined in Fig. 9b and the South America coastal El Niño warming events (Table 1), with the latter leading the former by about 4–8 mo (Horel and Wallace 1981).

Comparison of Table 1 (for the period 1951–76) and Fig. 9b reveals that during or just before the onset of an El Niño event, there is a swing in the SOI from positive to negative values (the years 1953 and 1965 are exceptions). The close relationship between the SO and El Niño, especially during major warmings, has lead to the coining of the term "El Niño – Southern Oscillation" events, or ENSO for short.

Phases and Mechanisms of a Typical El Niño – Southern Oscillation Event

Cold Phase

For about 18 mo before a "typical" ENSO event (the composite event of Rasmusson and Carpenter (1982), obtained by averaging the data from the 1951, 1953, 1957–58, 1965, 1969, and 1972–73 Los Niños), the Pacific trade winds blow intensely along the equator from the South Pacific high-pressure zone to the Indonesian–Australian low-pressure zone (Fig. 10a, 11a). In the latter zone, the warm moist air rises (creating a strong convection region) and returns eastward (at a height of 10–15 km), finally sinking over the cold dry South Pacific high. This zonally oriented circulation pattern in the tropical atmosphere is known as the Walker Circulation (Fig. 11a). In this atmospheric state, the SOI is positive (Fig. 9b).

The trades along the equator drive the westward-flowing South Equatorial Current (SEC) (Fig. 11a), which produces high sea levels and a large pool of warm water in the western tropical Pacific (typically 28–29°C water, with little annual variation). The thermocline below the SEC slopes downward towards the west, to a depth of about 150 m (Fig. 11b). In the eastern equatorial Pacific, the mixed layer is relatively thin (<50 m) and essentially disappears off the coast of South America. The return eastward flow below the thermocline is known as the Equatorial Undercurrent (EUC) (Fig. 11a). The tongue of relatively cool (20–24°C, with coldest temperatures in fall) surface water in the eastern equatorial Pacific (extending westward to 110°W, see Fig. 11b) is due to equatorial upwelling and to advection by the SEC of the cold coastal upwelled water off South America. West of 110°W, the SEC is strongly heated by the atmosphere.

There is also an important meridional atmospheric motion called the Hadley Circulation, which consists of two cells, one in each hemisphere. The Intertropical Convergence Zone (ITCZ) is the southern boundary of the Northern Hemisphere branch of the Hadley Circulation and the northern boundary of the southern branch of the Hadley Circulation. During summer (and a cold phase of ENSO), the ITCZ lies approximately along 10°N (Fig. 10a). Here the northeast and southeast trade winds meet and produce rising air which then flows to midlatitudes, sinking in the high-pressure zones off California and South America. The ITCZ is generally visible in satellite imagery, as it consists of a narrow band of cloud and rain. Another important meridional circulation is associated with the South Pacific Convergence Zone (SPCZ), located in the southwestern Pacific (Fig. 10a).

Development Phase

A number of substages are described in the literature (e.g. the precursor, onset, and growth stages) but there is often no

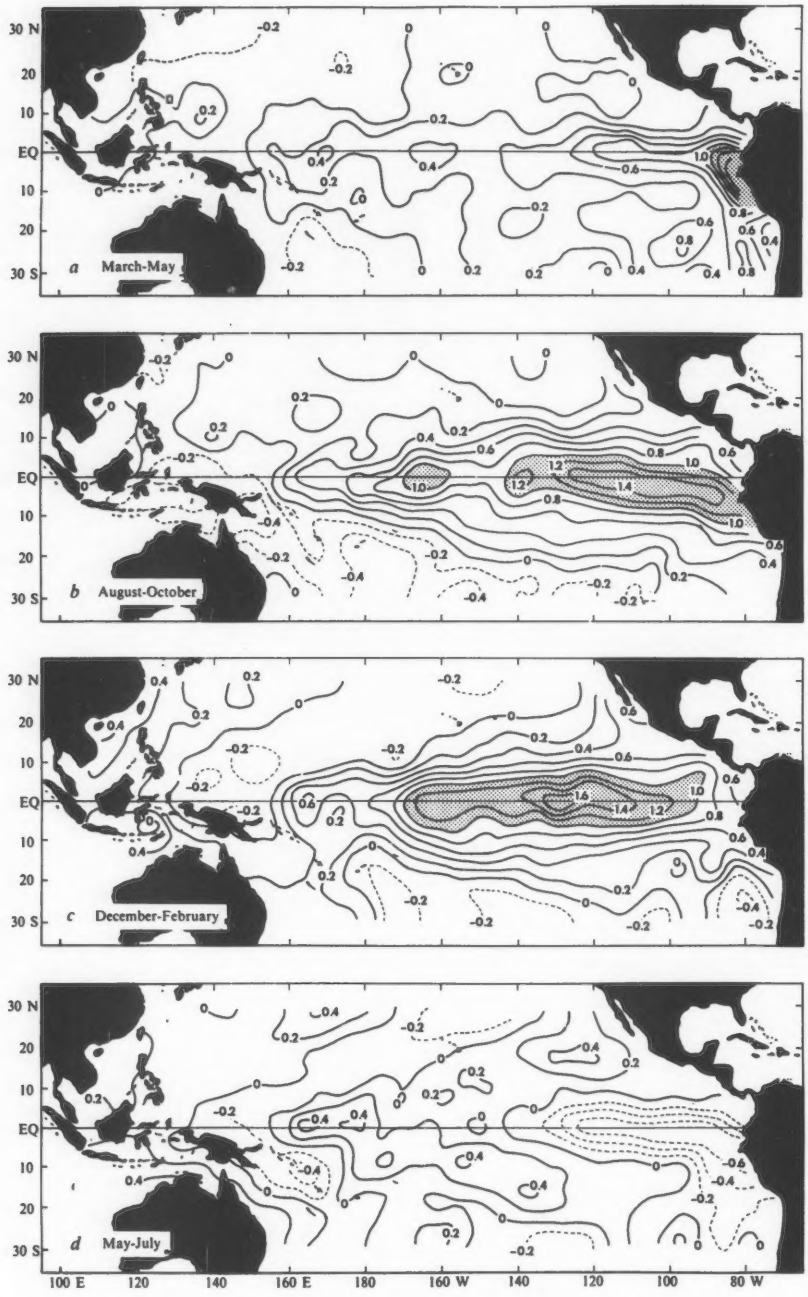


FIG. 8. Sea surface temperature anomalies (°C) during a typical (canonical) Pacific warming event obtained by averaging data for the six El Niño events between 1950 and 1973: 1951, 1953, 1957–58, 1965, 1969, 1972–73 (see Table 1 and note that the weak event of 1963 is omitted) (from Rasmusson and Carpenter 1982). (a) March, April, and May after the onset in January off the Ecuador–Peru coast; (b) the following August, September, and October; (c) the following December, January, and February; (d) May, June, and July, more than 1 yr after the onset in January of the preceding year.

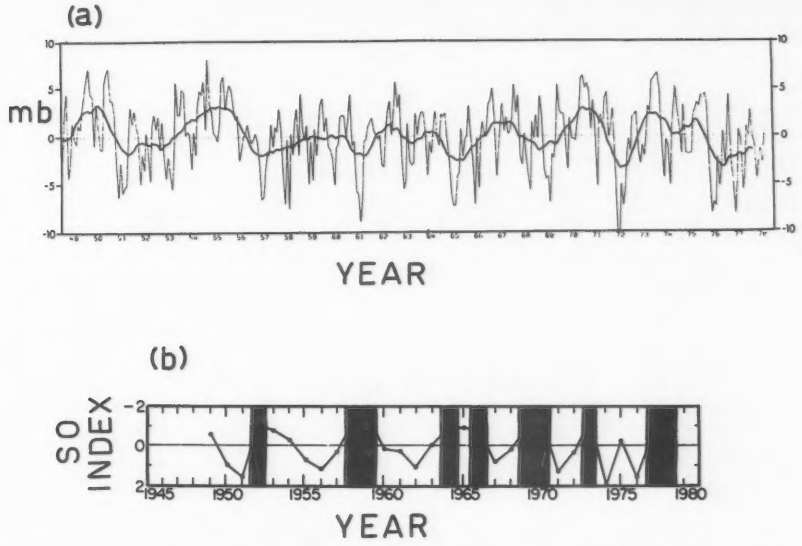


FIG. 9. (a) Southern Oscillation as given by the difference of atmospheric pressure between Easter Island (in the southeast Pacific) and Darwin, Australia, relative to a mean of 10.3 mb. The thin lines give monthly means, and the heavy line the 12-mo running mean (from Wyrtki 1982). (b) Time series of the Southern Oscillation Index (Tahiti minus Darwin normalized sea level pressure) as defined by Horel and Wallace (1981). The index has been inverted so that highs in the time series correspond to periods of anomalously warm sea surface temperatures (shaded) in the central equatorial Pacific as analyzed by Weare et al. (1976).

clear demarcation between one stage and another. One of the first precursors of a typical ENSO event is the movement in fall (October–November) of the Indonesian–Australian low (a region of high rainfall) toward the dateline, and the concomitant buildup of pressure over Indonesia and Australia. The SOI then changes to negative values (Fig. 9b), the region of rainfall moves eastward, and the trades west of the dateline relax. This change in the Walker Circulation could be caused by the presence, in early fall, of a warm SST anomaly in the western tropical Pacific (Rasmusson and Wallace 1983), or by interannual variations in the monsoon system in the Indian Ocean (U.S. Climate Research Committee 1983).

The dynamic coupling between the atmosphere and ocean in the western tropical Pacific is of central importance for the onset of ENSO. A warm SST anomaly in the west acts as a heat source for the atmosphere. As the air above the SST anomaly heats up and rises, surface winds converge into that region, which helps to relax the easterly trade winds there. This relaxation produces anomalous eastward-flowing ocean currents which redistribute heat in the ocean zonally. But this process produces an SST anomaly! Thus, the ocean and atmosphere in the tropical Pacific is best modelled as a coupled dynamical system involving two fluids: water and air. According to Philander et al. (1984), perturbations in such a system can be unstable provided there exist sufficiently large horizontal gradients in the basic state SST.

Just before the onset of an ENSO event, the ITCZ moves toward the equator early in the calendar year (Fig. 10b). This produces rain and weak trade winds along the equator, especially to the east of the dateline. Thus, the SEC slows down, permitting increased surface heating and a higher SST. The SPCZ, on the other hand, shifts northeastward before an ENSO event (Fig. 10b).

The autumn relaxation of the trades to the west of the dateline causes a drop in the sea level, a reduction in the strength of the SEC, and the generation of a series of downwelling equatorial Kelvin wave pulses (Wyrtki 1975; Busalacchi and O'Brien 1981; Knox and Halpern 1982; Eriksen et al. 1983; Luther et al. 1983; Cane 1984; Busalacchi and Cane 1985). The eastward propagation of each wave pulse causes the thermocline to drop and the sea level to rise to the east of the dateline (Fig. 12a). Moreover, east of the dateline, the wave amplitudes increase further due to reinforcement by trade wind relaxation in this region during the first part of the calendar year. Each wave pulse takes about 2 mo to cross the Pacific. Over a period of several months these waves effectively eliminate the climatological east–west slope of the thermocline along the equator (Fig. 11b). Also, at the eastern boundary in spring the sea level rises, the thermocline sinks, and a southward-flowing coastal current extending from the equator to southern Peru is formed.

A linear wave theory (e.g. Busalacchi and O'Brien 1981), while successfully explaining sea level height and thermocline depth changes, cannot account for the advection of warm water toward the coast of South America. If nonlinear and mixed-layer dynamics are included in the theory (e.g. Boyd 1980a; Philander 1981; Schopf and Harrison 1983; Harrison and Schopf 1984), warm water can be advected eastward by nonlinear wave pulses, which helps to produce a warm SST anomally off the South American coast. However, this feature can also be produced by reduced equatorial upwelling and net surface heating near the eastern boundary (Leetmaa 1983).

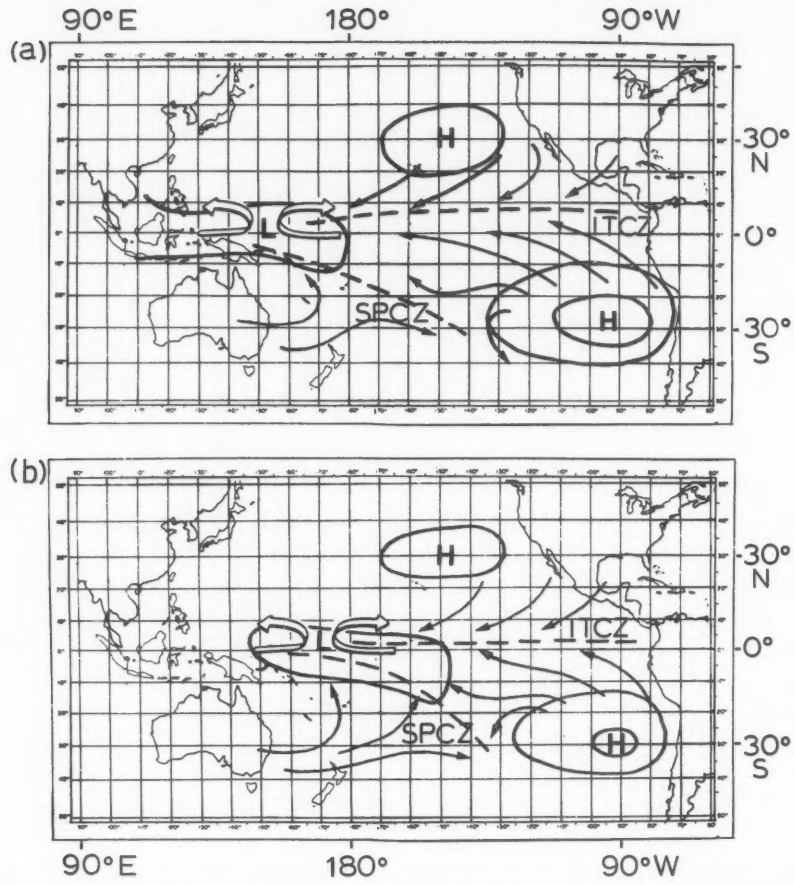


FIG. 10. Schematic depiction of atmospheric conditions during the two main phases of ENSO, corresponding to the (a) "cold phase" or normal conditions and (b) "warm phase." Sea level atmospheric pressure is shown by the solid contours and the surface wind flow by solid arrows. The locations of the Intertropical Convergence Zone (ITCZ) and South Pacific Convergence Zone (SPCZ) are indicated by broken lines. The rising portion of the Walker Circulation is marked by the open arrows. (Adapted from U.S. Climate Research Committee 1983.)

Warm Phase

The extremely deep thermocline depression and high sea level which occur at the South American coast during spring are believed to be due to a resonance between two sets of equatorial Kelvin waves that arrive simultaneously — those generated west of the dateline during late fall and those generated east of the dateline during January–February (Busalacchi and O'Brien 1981). However, the extreme warming at the coast, with peak SST occurring in April–May (Fig. 13a), is caused mostly by local heating of the thick mixed layer above the thermocline (Weare 1983).

The expansion of the anomalously warm coastal water westward during summer and fall (Fig. 8b) could be caused by advection associated with westward-travelling equatorial Rossby waves (LeBlond and Mysak 1978, Chap. 3) that are generated at the coast by the incident Kelvin waves (Semtner and Holland 1980). Such waves are nondispersive and, in the absence of air–sea heat exchanges, travel with a phase speed of about one third that of the Kelvin waves, i.e. about 75 $km \cdot d^{-1}$. Such relatively slow-moving waves are likely to be significantly affected by nonlinearity which allows for the westward advection of warm water (Boyd 1980b; Greatbatch 1985).

Warm surface water can also move westward by nonwavelike processes, such as air–sea interactions. Horel (1982) argued that the rising air over a warm patch of water produces a wind component toward the east (relative to the mean) on the western side of the patch. This would produce Ekman convergence in the ocean and hence downwelling. On the eastern side of the patch the easterly trades would be strengthened, resulting in Ekman divergence and upwelling. Consequently, the water is heated at the western boundary and cooled at the eastern boundary, and the whole patch is seen to move westward. A similar effect can also be produced by changes in the stress and heat flux associated with the passage of the air over a warm patch of ocean water (Kraus and Hanson 1983).

The westward moving warm SST anomaly finally merges in November–December with the SST anomaly that was initially

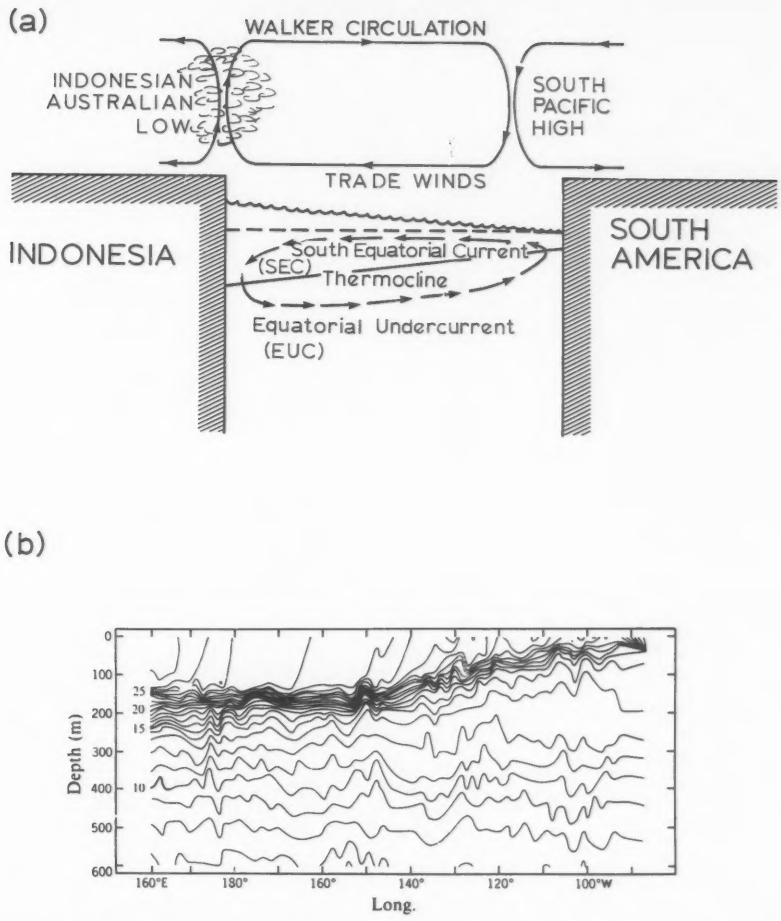


FIG. 11. (a) Schematic representation of the ocean currents driven by the easterly trade winds along the equator. The clouds shown in the Indonesian–Australian low pressure region indicate an area of heavy rainfall. (b) Temperature (°C) as a function of depth and longitude along the equator in the Pacific Ocean (Colin et al. 1971). The 15° isotherm marks the base of the thermocline.

present west of the dateline (Fig. 8b, 8c). The creation of this very large equatorial pool of warm water extending a quarter of the way around the circumference of the earth marks the mature phase of an ENSO event. The trades are very weak, and west of the dateline there are westerlies, which bring anomalous rainfall to the central Pacific. Because the ITCZ is now farther south (near the equator), the Hadley Circulation is also altered (the meridional flow is accelerated). The latter feature, together with the large equatorial SST anomaly in late fall – early winter, have significant impacts upon the midlatitude winter atmospheric circulation. The details of these are discussed further in "Midlatitude Effects of an ENSO Event."

Dissipation Phase

After peaking in April–May, the SST anomaly off the coast of South America declines rapidly, although in some years (e.g. 1957 and 1972) there is a second, but weaker warming which begins in September–October and extends through to January–February of the next year. These two second warmings produce the second peak centered at December in the composite SST curve of Fig. 13a. Since the ENSO events which began in January of 1957 and 1972 lasted through to spring of the following year, they have been given a double year designation in Table 1, i.e. 1957–58 and 1972–73. By March of the second year, the coastal water of the composite event is cool, and by May, the SST along the equator is anomalously cool in a long tongue which extends from the South American coast out to 140°W (Fig. 8d). Also, by spring of the second year, the western upward-rising branch of the Walker Circulation shifts back to Indonesia, the SOI swings toward positive values, and the easterly trades prevail across the tropical Pacific. Such steady trade winds once again set up the westward sea level slope, the tilted thermocline (Fig. 11b), and a strong SEC (Fig. 11a), bringing us back to the cold phase.

Time Interval between Events

An open question is "What determines the time interval between successive ENSO events?" One view is to regard the

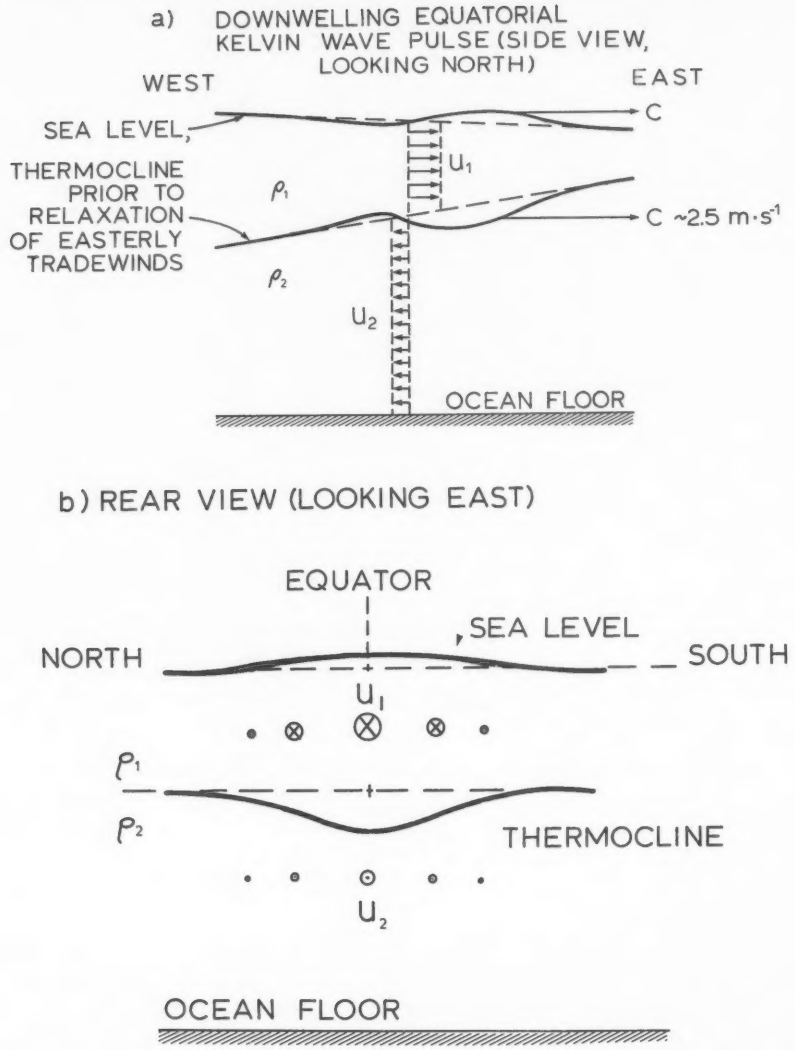


FIG. 12. (a) Side view of a downwelling equatorial Kelvin wave pulse in a two-layer ocean generated by a relaxation of the easterly tradewinds. Note that the wave-induced currents in each layer are in opposition to the climatological mean South Equatorial Current (SEC) (which flows westward in the upper layer) and Equatorial Undercurrent (EUC) (which flows eastward in the lower layer). For strong Kelvin wave pulses with $u_1 \sim 1$ m·s^{-1}, the SEC, which is generally < 1 m·s^{-1} in magnitude, can be locally reversed, as happened in August 1982 during the 1982–83 ENSO event (Halpern et al. 1983). Similarly, the EUC can locally disappear because of Kelvin wave pulses (Firing et al. 1983). (b) Rear view of equatorial Kelvin wave showing Gaussian-shaped trapping region, which is proportional to $\exp(-y^2/r_e^2)$, where y is the distance north of the equator and r_e is the first baroclinic mode Rossby radius for the equator (typically $r_e = 300$ km (Moore and Philander 1977)).

occurrence of ENSO events as a random process, with the various precursors falling into place by chance, but possibly aided by irregular (interannual) fluctuations in the Indian monsoon system (U.S. Climate Research Committee 1983). A second view assumes that ENSO events are part of a continuous cycle, and that with the decay of one event, the seeds are sown for the birth of another. McCreary (1983) (see also McCreary and Anderson 1984) argued that the time interval between events is mainly determined by the time taken for an ENSO-generated *subtropical* baroclinic Rossby wave to travel westward across the Pacific. Such a wave is believed to be generated as follows. With the development of SST anomalies in the western equatorial Pacific, the easterly trades relax and generate an eastward-travelling downwelling equatorial Kelvin wave (i.e. an ENSO event "begins"). When this wave strikes the eastern boundary, it is partly transformed into poleward-travelling coastal Kelwin waves (Fig. 14). At low or middle latitudes (15–30°N or S), these coastal Kelvin waves radiate

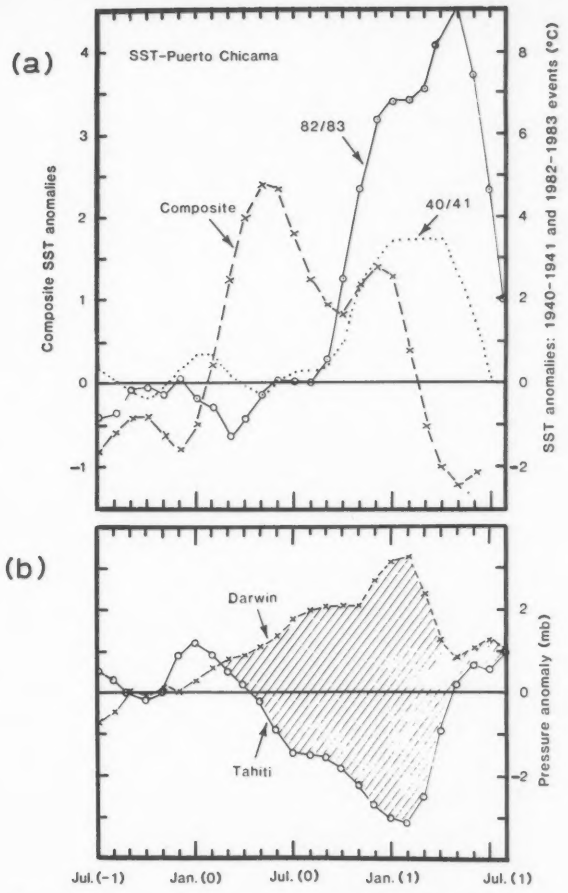


FIG. 13. (a) Three-month running mean SST anomalies for Puerto Chicama, Peru (7.7°S, 79.3°W). Continuous and dotted lines refer to the 1982–83 and 1940–41 episodes, respectively. For these two curves, year 0 on the abscissa refers to 1982 and 1940, respectively. The broken curve refers to a composite of six warm episodes between 1950 and 1975. The ordinate scales for the 1982–83 and 1940–41 events (right) represent SST anomalies twice as large as those represented by the corresponding scale (left) for the composite event. (b) Sea level pressure anomalies at Tahiti (17°S, 150°W) and Darwin (12°S, 131°E) during the 1982–83 episode. The difference between the two air pressures (Tahiti minus Darwin), indicating by shading, is often used as an index of the Southern Oscillation (see Fig. 9b). (From Rasmusson and Wallace 1983.)

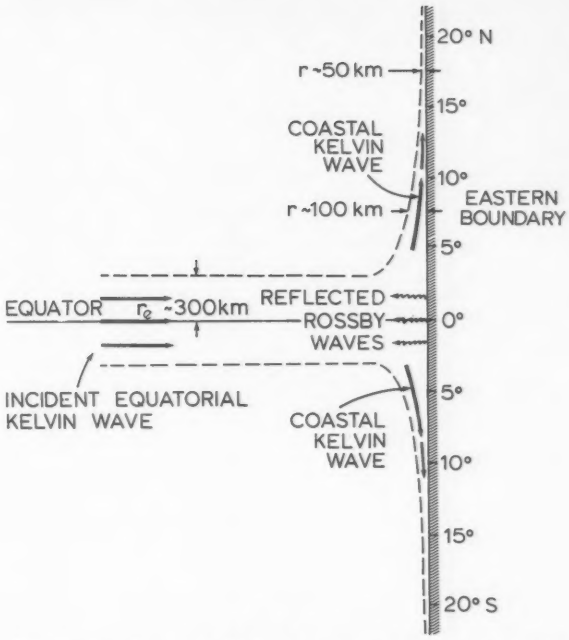


FIG. 14. Transformation of a first baroclinic mode equatorial Kelvin wave into westward-travelling equatorial Rossby waves and poleward-travelling coastal Kelvin waves. The broken lines indicate the approximate boundaries of the equatorial and coastal wave guides, as determined by the equatorial and midlatitude internal Rossby radii, r_e and r. The latter radius r diminishes rapidly away from the equator: at ±25°, $r \sim 35$ km; at ±45°, $r \sim 20$ km; at ±55°, $r \sim 12$ km (Emery et al. 1984).

(i.e. scatter) a significant portion of their energy into baroclinic Rossby waves which propagate slowly along the sub-tropical thermocline (Fig. 15) toward the western side of the Pacific (White and Saur 1983; Magaard 1983). At 15°N or S the transit time for such a baroclinic Rossby wave is 2 yr; at 30°N or S it is 9 yr (McCreary 1983). At the western boundary these waves generate equatorward-travelling coastal Kelvin waves (Fig. 2) which reach the equator in a few months, and which help create the SST anomalies west of the dateline that herald the beginning of another ENSO event. (White and Pazan (1985) showed that this was indeed the case prior to the 1982–83 event.) Since the transit times of the equatorial and coastal Kelvin waves are on the order of a few months, it is the transit time of the subtropical Rossby waves which largely determines the time interval between ENSO occurrences, i.e. 2–9 yr.

A third possible explanation for the irregular occurrence of ENSO events is based on the stability of coupled ocean–atmosphere models. For the initiation and growth of SST anomalies, certain stability conditions have to be satisfied, and according to Hirst (1985) and Rennick and Haney (1985), this happens infrequently.

Anomalous El Niño of 1982–83

The recent 1982–83 ENSO episode evolved in an unusual manner (Kerr 1983; Philander 1983), but had a structure which may have been similar to the poorly documented but strong 1940–41 event (Rasmusson and Wallace 1983). Instead of a warming first appearing off Peru and Ecuador in spring and then expanding westward in summer and fall, a large, very warm SST anomaly first formed in the western Pacific in May–June 1982 and then expanded eastward, reaching the South American coast by September 1982. The SST off Peru then rose rapidly, reaching temperatures of 6–8° above normal by May–June of 1983 (Fig. 13a). Also during September–October 1982 the sea levels along the Ecuador–Peru coastline began to rise precipitously (Cane 1983). The warming off Peru–Ecuador persisted through to the summer of 1983, whereas a typical ENSO event would have ended there in March.

The eastward expansion of the warm SST anomaly during spring and summer 1982 was accompanied by an eastward

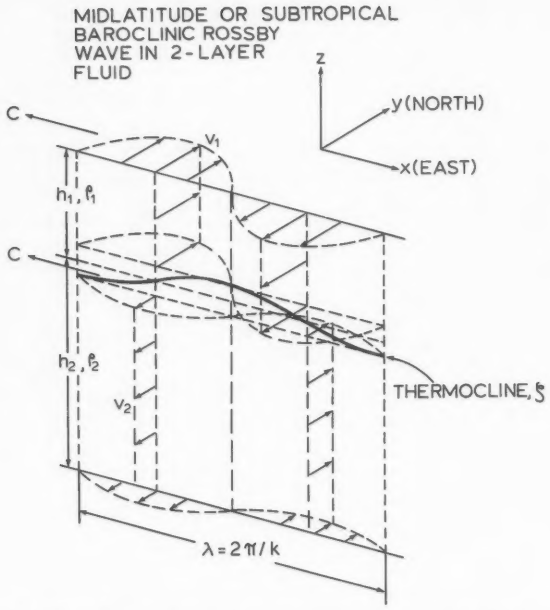


FIG. 15. Velocity and thermocline structure of a westward-travelling baroclinic Rossby wave in a two-layer ocean. For the upper-layer y-velocity component

$$v_1 = V \cos k(x - ct),$$

the lower-layer y-velocity component and thermocline displacement are given by

$$v_2 = -(h_1/h_2)v_1$$

$$\zeta = (fV/g'k) \sin k(x - ct),$$

where $c = -\beta/(k^2 + r^{-2})$ is the phase speed (r is the internal Rossby radius), $\lambda = 2\pi/k$ is the wavelength, $g' = g(\rho_2 - \rho_1)/\rho_2$ is the reduced gravity, and f is the Coriolis parameter, with $\partial f/\partial y = \beta$. Note that in contrast with Kelvin waves, Rossby waves are transverse, i.e. the current fluctuations are perpendicular to the direction of phase propagation.

FIG. 16. Schematic illustration of atmospheric circulation anomalies at 5–10 km (the jet stream level) during Northern Hemisphere winter after the peak of an ENSO episode in the equatorial Pacific. The wavy broken line with arrows lying between 30 and 60°N depicts an actual streamline as distorted by the anomaly pattern. The region of enhanced precipitation (which overlies a large SST anomaly) is shaded. The H-L-H-L pattern stretching across the North Pacific, western Canada, and the southeastern United States is known as the Pacific/North American (PNA) teleconnection pattern (Horel and Wallace 1981).

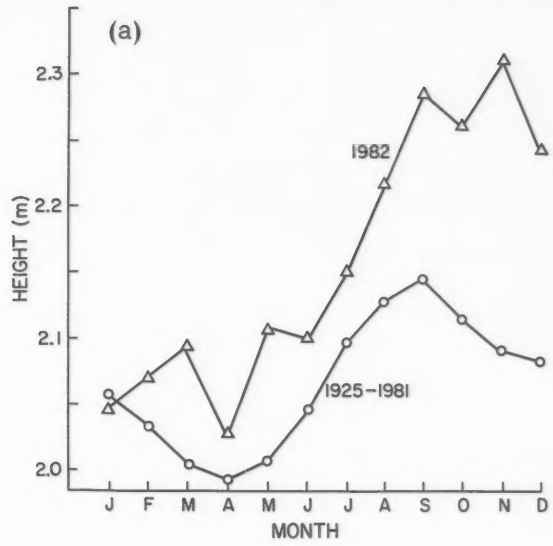
movement of the Indonesian–Australian low well beyond the dateline, resulting in record low values of the SOI in January 1983 (Fig. 13b). This extreme change in the Walker Circulation contributed to drought in the far western Pacific, late monsoons over the Indian Ocean, and cyclones and excessive rainfall in the Polynesian islands. Also, the easterly trades were replaced by westerly winds which moved eastward across the Pacific. With the excessive evaporation due to the high SST off Peru and Ecuador, catastrophic flooding occurred there during (northern) winter 1982–83. By May 1983, the convective region had shifted back towards Indonesia, the SOI was close to zero (Fig. 13b), and the easterly trades returned. Water temperatures off the South American coast returned to normal in August 1983.

For a detailed discussion of the biological response in the eastern tropical Pacific to the 1982–83 event, see Barber and Chavez (1983).

Midlatitude Effects of an ENSO Event

Shortly after the mature phase of a strong ENSO event at the end of a calendar year, the oceanic response off the California – British Columbia coast consists of high sea levels (especially during winter), warm SST's (winter and spring), and low salinities (winter and spring). Although these anomalies persist for only one or two seasons, they are sufficiently large to produce anomalous annual mean values (as in Fig. 1, 3, and 4). Also during winter–spring following the mature phase of ENSO, the equatorward flow off California (the offshore California current) is reduced (Chelton et al. 1982) and the poleward flow along the Oregon – British Columbia and Alaskan coasts (the Davidson Current) is intensified (Emery et al. 1985). The latter is an extension of the inshore California countercurrent which tends to increase in fall during an ENSO event (J. J. Simpson, Scripps Institution of Oceanography, La Jolla, CA, pers. comm.). Two mechanisms have been proposed to explain the occurrence of these midlatitude anomalies: (i) the coastal wave guide along the eastern boundary (McCreary 1976; Enfield and Allen 1980; Fig. 14) and (ii) the Pacific/North American (PNA) teleconnection in the troposphere (Horel and Wallace 1981; Hoskins and Karoly 1981; Fig. 16).

The extensive work on coastal trapped wave theory and observation (see the review by Mysak (1980)) has biased the thinking of the oceanographic community toward the first mechanism. However, as ENSO events become better documented and understood, several shortcomings of this oceanic wave guide mechanism emerged. Today, the teleconnection mechanism, in which ENSO-induced anomalies in the atmospheric circulation play an integral role, is more favored and certainly played a major role in producing the warming and



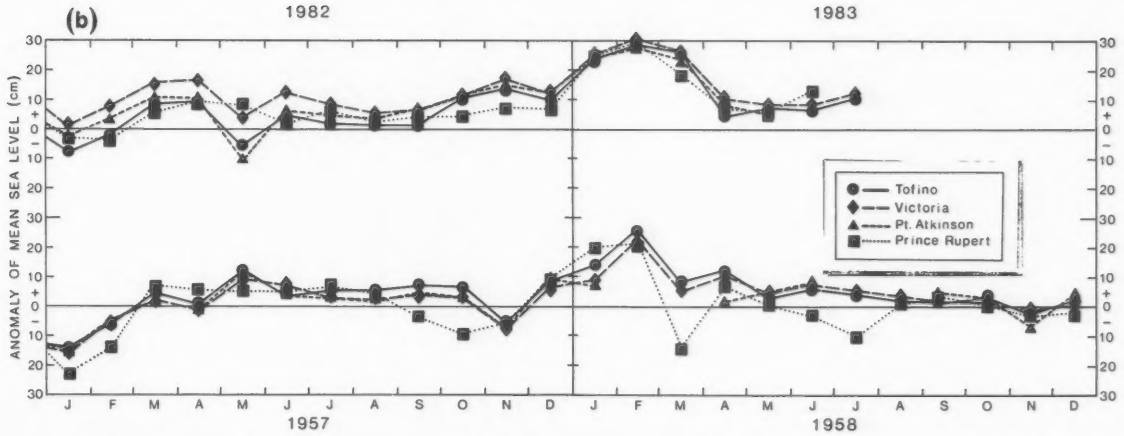


FIG. 17. (a) Monthly mean sea level from Scripps Pier, La Jolla, California, during 1982 (Simpson 1983). (b) Anomaly of 1957–58 and 1982–83 monthly mean sea level heights from four British Columbia coastal stations: (from south to north) Victoria, Tofino, Point Atkinson (West Vancouver), and Prince Rupert (Tabata 1984a).

anomalous currents in the northeast Pacific Ocean during the 1982–83 event.

Coastal Wave Guide

Figure 14 shows that when an equatorial Kelvin wave reaches an eastern boundary, it is partly transformed into two poleward-travelling coastal Kelvin waves (Fig. 2). However, the continental shelf, whose width L_s is typically 50 km, can significantly affect the poleward-travelling Kelvin waves, since the trapping scale r (internal Rossby radius) of these waves diminishes with latitude (Fig. 14; Emery et al. 1984). At very low latitudes, $r \gg L_s$ and the shelf has a negligible effect. However, at higher latitudes, $r \sim L_s$ and the shelf can play an important role. If the thermocline lies below the shelf break, a poleward-travelling Kelvin wave will eventually disappear as an internal disturbance and transform into a barotropic (depth-independent) shelf wave that is trapped over the shelf (Suginohara 1981). Such waves travel in the same direction as Kelvin waves, at a phase speed of $c = 100 - 300$ km·d^{-1} (Mysak 1980; Yao et al. 1984). On the other hand, if the thermocline lies over the shelf and intersects a shallow coastal wall, then an internal Kelvin wave will persist at high latitudes (Suginohara 1981).

In the eastern tropical Pacific, the first situation generally prevails during ENSO, so that thermocline depressions at low latitudes will travel poleward as internal coastal Kelvin waves. Such wave disturbances, with a phase speed of 200 km·d^{-1}, have been observed off Peru (Brink 1982; Smith 1983). As a low-latitude internal Kelvin wave travels northward along the west coast of North America, it will be transferred into a barotropic wave signal (Suginohara 1981) which would be observed in the sea level fluctuations. But substantial mid-

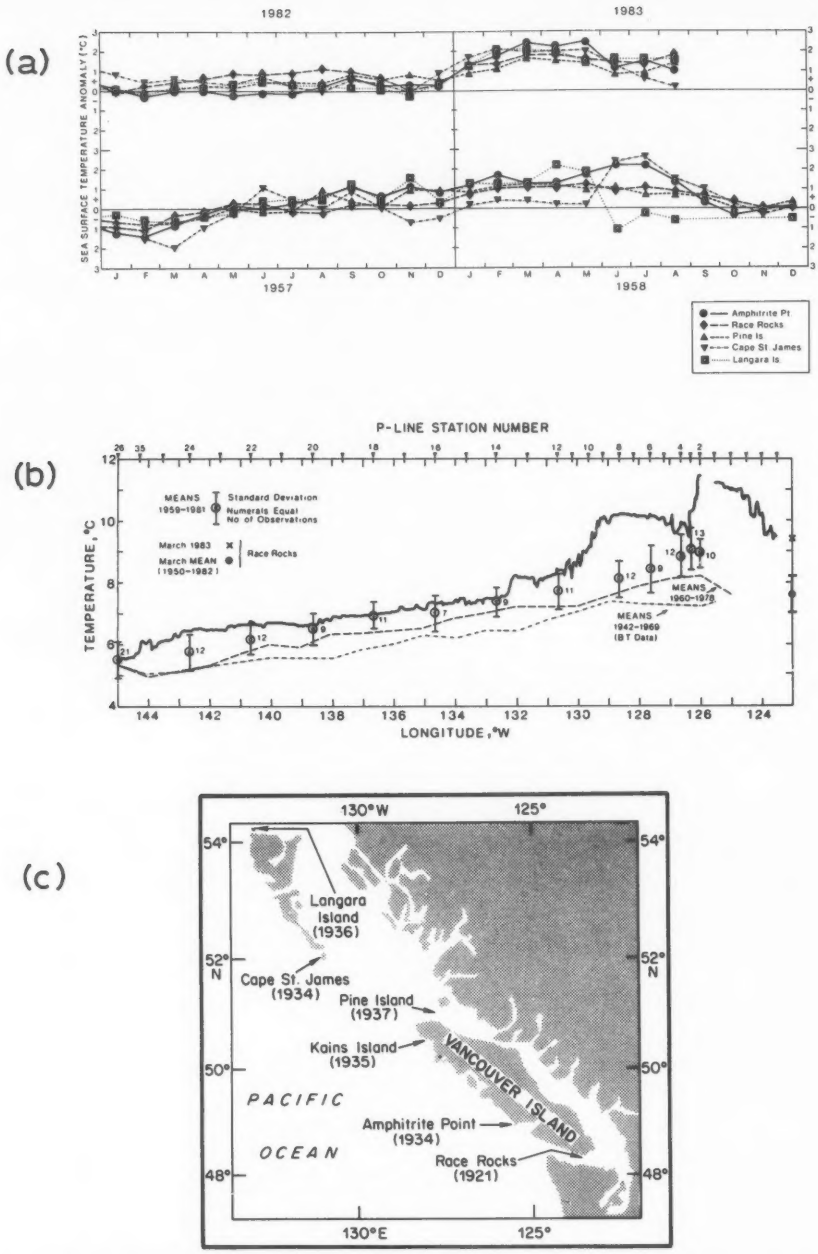


FIG. 18. (a) Anomaly of 1957–58 and 1982–83 monthly SST from five exposed British Columbia coastal stations: (south to north) Race Rocks, Amphitrite Point, Pine Island, Cape St. James, and Lanagara Island (Tabata 1984a). The station locations are shown in Fig. 18c. (b) Sea surface temperature along Line P during 16–20 March 1983 (Tabata 1984b). (c) Locations of coastal SST monitoring stations used in Fig. 18a and in Fig. 35 (Thomson et al. 1984).

latitude thermocline disturbances and other baroclinic anomalies (e.g. SST anomalies) would not likely be caused by such a wave.

Another important oceanic feature which will seriously inhibit internal Kelvin wave propagation poleward is the surfacing of the thermocline (~15°C isotherm) at some extratropical latitude (about 30°). An internal Kelvin wave travelling poleward along an upward sloping thermocline will cease to exist as an internal disturbance beyond that critical latitude where the thermocline intersects the surface. Since a coastal Kelvin wave

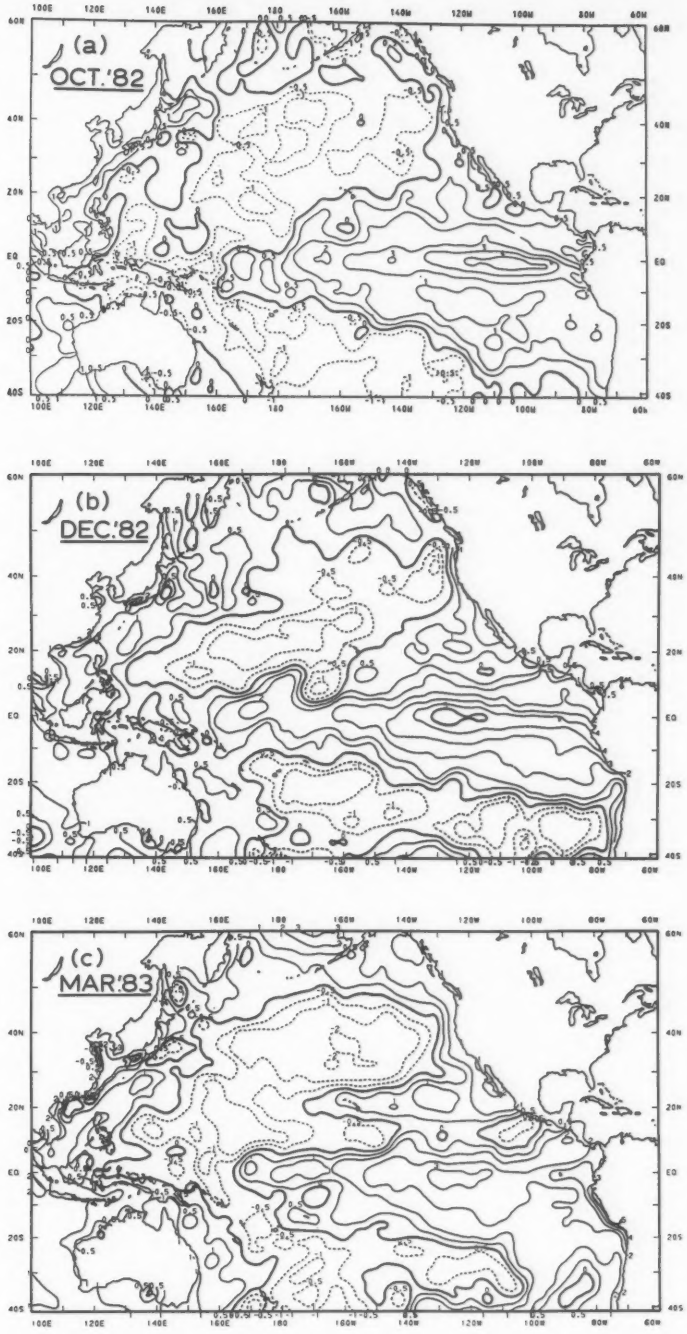


FIG. 19. Sea surface temperature anomalies (°C) for (a) October 1982, (b) December 1982, and (c) March 1983 (Climate Analysis Center, NOAA, Washington, DC.).

(at subinertial frequencies) cannot be reflected there, it is likely transformed into a westward-travelling baroclinic Rossby wave (Fig. 15).

The 1982–83 sea level and SST data along the west coast of North America are now examined in relation to coastal trapped waves. The 1982 monthly sea levels at La Jolla, California (Fig. 17a), began to rise in summer and peaked in November. This rise preceded the increase in sea levels along the

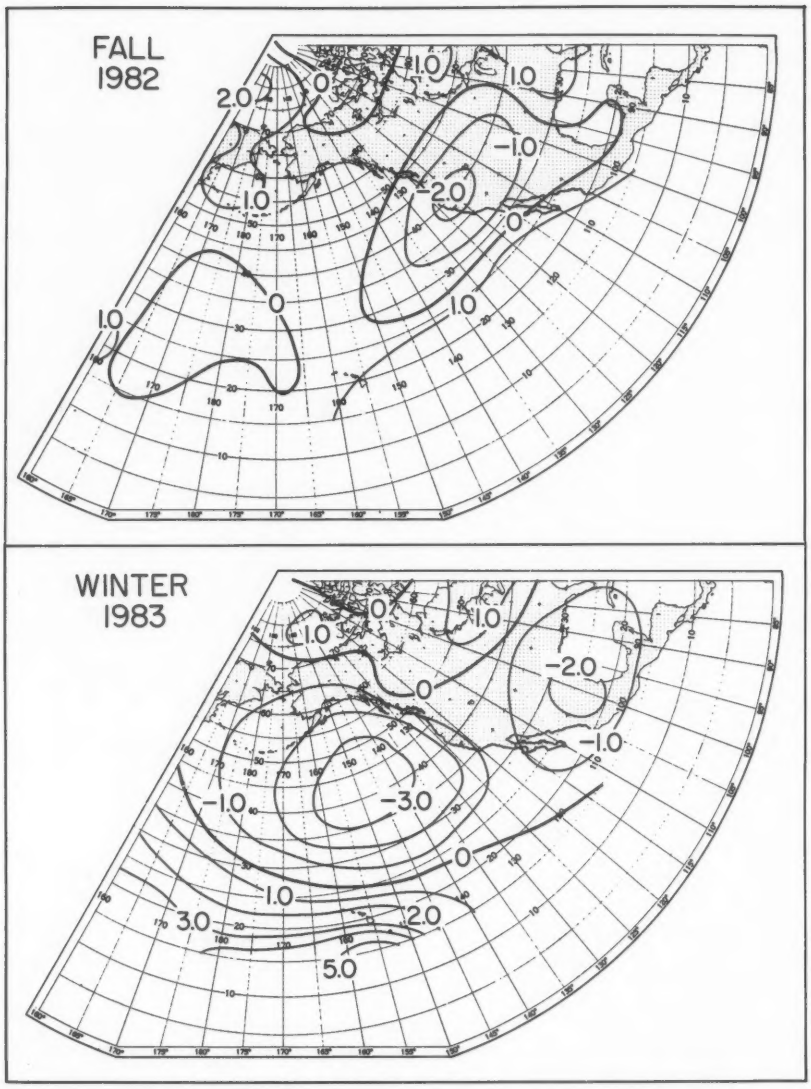


FIG. 20. Anomalies of 700-mb height (seasonal mean) from 26-yr climatological mean plotted in units of the standard deviation σ (Simpson 1983).

Ecuador–Peru coast, which occurred in September–October (Cane 1983). This sea level time evolution is just the opposite to what one would expect for northward-travelling waves between Ecuador (on the equator) and California. On the other hand, the sea level off British Columbia (Fig. 17b) peaked in February, about 3 mo after the peak observed at Scripps pier. The wave phase speed corresponding to such a time lag is roughly 20 $km \cdot d^{-1}$, which is about one tenth the speed of a coastal trapped wave. The anomalous rises of the sea level off British Columbia during the winters of 1958 and 1983, together with the gradual rises during winter–spring of each of the previous years, suggest that the British Columbia sea level response during ENSO may rather be viewed as an amplification of the seasonal pattern of sea level changes due to anomalous atmospheric forcing.

Figure 18a shows that the extreme warming in the northeast Pacific began in November–December 1982 but did not peak until spring 1983 (well after the sea level peak in February). This warming coincided with that which occurred off Peru (Fig. 13a), a fact which negates the idea of internal Kelvin waves carrying the warm equatorial water northward. Finally, Fig. 18b shows that the offshore scale of the March SST warming along Line P (at ~50°N) extended offshore about 300 km. At the same time, there was also considerable sub-

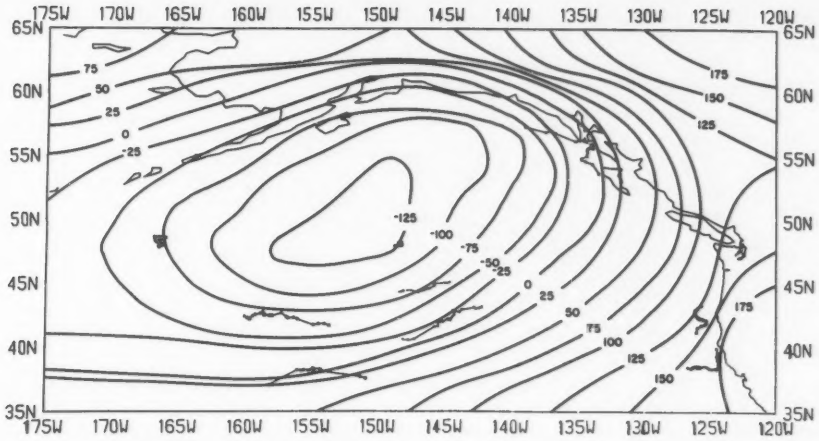


FIG. 21. Monthly mean sea level pressure (×0.1 + 1000 mb) for January 1983. Also shown are the corresponding monthly portions of the satellite-tracked-drogued buoy tracks (Emery et al. 1985).

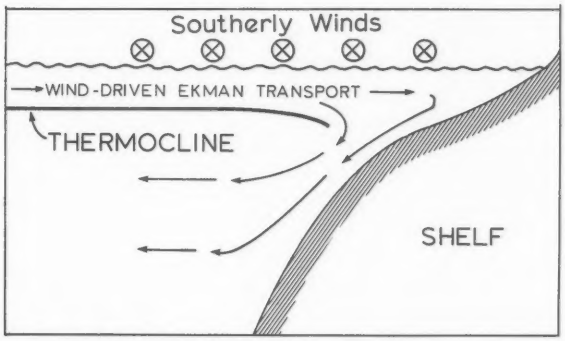


FIG. 22. Downwelling along the British Columbia coast due to southerly longshore winds.

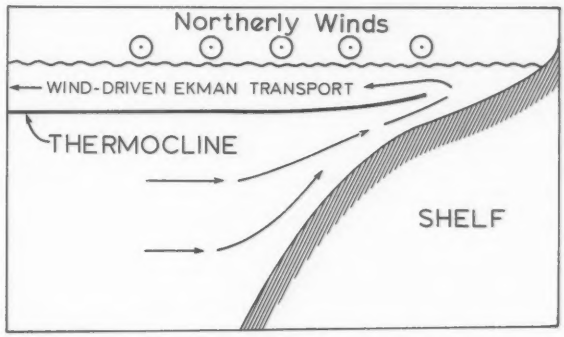


FIG. 23. Upwelling along the British Columbia coast due to northerly longshore winds.

surface warming off Vancouver Island (Tabata 1984b). Off California, the maximum warming (4° above normal) occurred at a depth of 100 m, and at a distance of 100–200 km offshore (Simpson 1983). In both regions the horizontal extent of the coastal warming far exceeds the local internal Rossby radius, and hence provides further evidence that internal Kelvin waves were not involved in determining the horizontal scale of this anomaly.

The temporal development (fall 1982 to spring 1983) of the SST anomalies for the entire Pacific Ocean is illustrated in Fig. 19. Anomalous warming along the west coast of the United States and British Columbia began to develop around October 1982 (Fig. 19a); at the same time, a large cold SST anomaly in the central Pacific began to form. By March 1983 the cold anomaly had shrunk slightly in size, and at the eastern boundary in the Northern Hemisphere there was little evidence of northward propagation of the temperature anomaly, but rather a broadening of the coastal band of warm water (1–2° above normal) out to 500 km or so along the California – British Columbia coast. However, a careful scrutiny of the anomaly patterns in Fig. 19a, 19b, and 19c reveals that the maximum warming off British Columbia tended to occur about 3–4 mo after the peak warming in the central equatorial Pacific (see also Pan and Oort 1983).

Pacific/North American Teleconnection

The intense heating of the tropical troposphere during the mature phase of ENSO produces an enchanced region of rainfall in the central equatorial Pacific which perturbs the Hadley circulation and generates a pattern of quasi-stationary Rossby waves at heights of 5–10 km. In the absense of mean winds, Rossby waves travel with a westward component and hence would produce little effect on midlatitude conditions in the atmosphere over the northeast Pacific Ocean. But in the Northern Hemisphere such waves can be advected vast distances to the northeast provided strong westerly winds prevail in a zonal band extending from the equatorial region to midlatitudes. Such mean wind conditions generally occur during the winter, which explains why the observed PNA teleconnection pattern shown in Fig. 16, which can be attributed to the advected Rossby waves, exists only during this season.

The patterns marked H and L in Fig. 16 are the regions over which the surface of constant pressure at an altitude of about 5 km is anomalously high (H) or low (L) and are referred to as the "centers of action." The H and L regions can also be interpreted as the peaks and troughs of the Rossby wave pattern

FIG. 24. Schematic depiction of the teleconnection patterns of Wallace and Gutzler (1981) and their respective centres of action (see Table 2) (Blackmon et al. 1984).

TABLE 2. Summary of the teleconnection patterns identified in Wallace and Gutzler (1981). The "centres of action" A, B. . . . , N are shown in Fig. 24.

Point label	Geographical position	Pattern name
A	(20°N, 160°W)	Pacific/North American
B	(45°N, 165°W)	
C	(55°N, 115°W)	
D	(30°N, 85°W)	
E	(25°N, 25°W	Eastern Atlantic
F	(55°N, 20°W)	
G	(50°N, 40°E)	
H	(55°N, 55°W)	Western Atlantic
I	(30°N, 55°W)	
J	(60°N, 155°E)	Western Pacific
K	(30°N, 155°E)	
L	(55°N, 20°E)	Eurasian
M	(55°N, 75°E)	
N	(40°N, 145°E)	

emanating from the equator. The high-pressure anomaly over Hawaii represents a perturbation of the Hadley Circulation. The low-pressure anomaly in the Gulf of Alaska leads to the

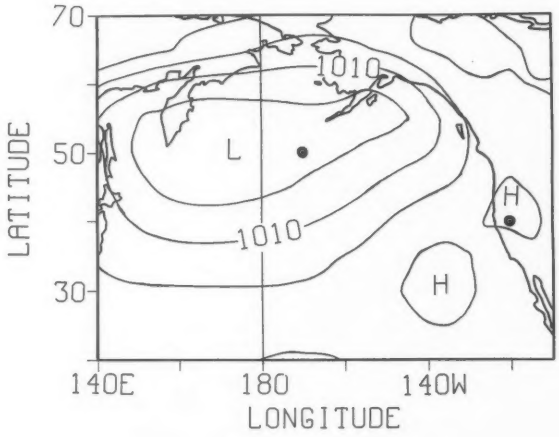


FIG. 25. Winter climatological sea level atmospheric pressure over the North Pacific for the 36-yr period 1947–82 (Emery and Hamilton 1985). Contours are in millibars and the contour interval is 5 mb. The North Pacific atmospheric pressure index (shown in Fig. 27 for the above 36-yr period) is defined as the winter mean sea level pressure at 40°N, 120°W (marked by the dot over California) minus the same at 50°N, 170°W (marked by the dot southwest of the Aleutian Islands).

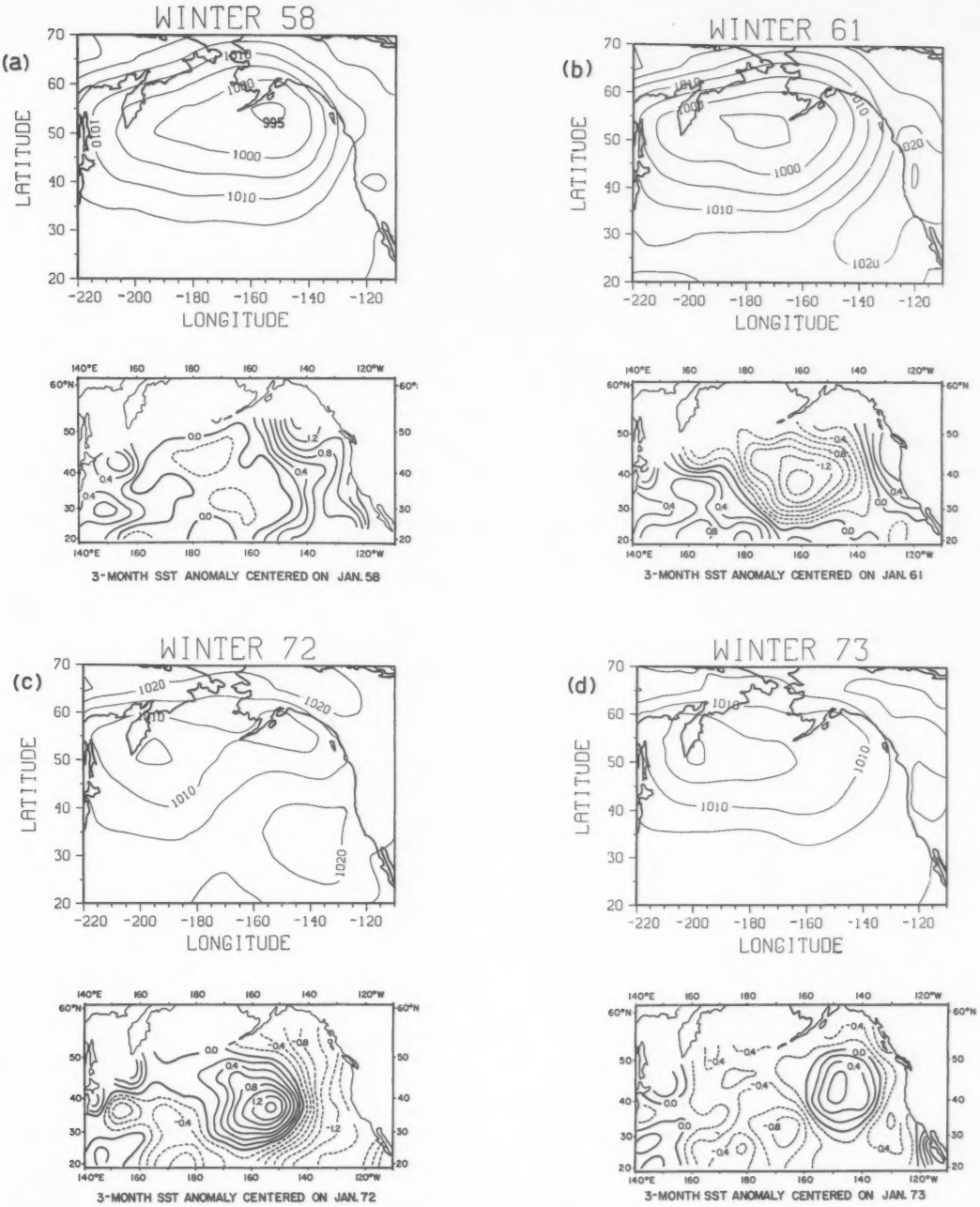


FIG. 26. Winter mean sea level atmospheric pressure and SST anomaly for (a) 1958, (b) 1961, (c) 1972, (d) 1973, and (e) 1977 (Emery and Hamilton 1985). (*Fig. 26 concluded next page*)

deepening and intensification of the Aleutian low, which produces anomalous winter–spring ocean conditions in the northeast Pacific. The high-pressure anomaly over western Canada is associated with low winter temperatures in Alberta, for example, and the low over southeastern United States results in high surface temperatures in that region. Also, these centers mark the locations of strong temporal correlations between tropical and extratropical climate anomalies (Horel and Wallace 1981; van Loon and Madden 1981; Rasmussen and Wallace 1983). The basic theoretical concepts underlying these correlations first appeared in the meteorological literature during 1970's (e.g. Hoskins et al. 1977), but the relevance to

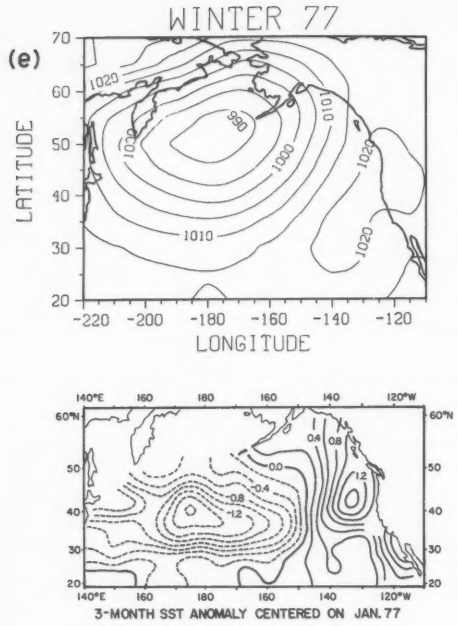


FIG. 26. (*Concluded*)

ENSO events was only identified during this decade (e.g. Hoskins and Karoly 1981; Webster 1981).

A number of simple models have recently been developed to study the dynamics of Rossby wave trains emanating from a region of enhanced tropical precipitation. The theoretical results indicate the following:

(i) The magnitude of the extratropical response due to the Rossby waves is increased by the presence of the climatological mean[2] stationary (time-independent) wave field that is forced by mountain ranges and land–sea temperature contrasts (Webster and Holton 1982).

(ii) During Northern Hemisphere winter, the atmospheric response takes the form of a geographically fixed pattern resembling Fig. 16, independent of the location of the equatorial heat source. This pattern is a normal mode associated with barotropic (a north–south shear) instability of the climatological mean zonal wind and may also be excited by mechanisms other than an equatorial heat source (Simmons et al. 1983). This is one possible explanation for the occurrence of PNA patterns similar to Fig. 16 (and associated northeast Pacific Ocean warmings) in years in which there is no equatorial ENSO episode, such as in 1961 (Emery and Hamilton 1985).

Anomalous conditions in the North Pacific Ocean following the mature phase of a strong ENSO episode are largely produced by the intensification and expansion of the climatological Aleutian low during winter and the simultaneous weakening and southward displacement of the climatological North Pacific high. These anomalous atmospheric conditions correspond to the L–H pattern in the North Pacific depicted in Fig. 16. Figure 20 shows the seasonal mean anomalies of the 700 mb height for fall (September – November) 1982 and winter 1983 (December 1982 – February 1983) over the North

[2]That is, the mean obtained by averaging over many years.

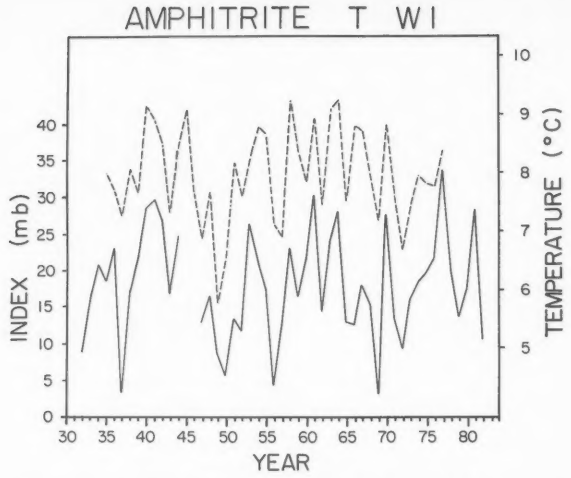


FIG. 27. Time series of the winter North Pacific atmospheric pressure index (solid line) (see caption to Fig. 25) and the observed winter mean SST at Amphitrite Point, British Columbia, (broken line) (Emery and Hamilton 1985).

TABLE 3. Classification according to Emery and Hamilton (1985) of the observed winter mean sea level atmospheric pressure patterns which are shown in Fig. 21 (1983) and 26 (1958, 1961, 1972, 1973, 1977). The strength of the circulation in each year is given relative to the winter climatological circulation implied by Fig. 25. The symbols A and B refer to the North American west coast (40–60°N) winter mean SST as being above normal or below normal. The labels C and W denote tropical cold and warm episodes in the eastern tropical Pacific (van Loon and Madden 1981; Pan and Oort 1983).

Weak N. Pacific atmospheric circulation	Near-normal N. Pacific atmospheric circulation	Strong N. Pacific atmospheric circulation
		1958, A, W
		1961, A
1972, B, C		
	1973, B, W	
		1977, A, W
		1983, A, W

Pacific. The negative contours over the central North Pacific during winter indicate that during the last ENSO event, the Aleutian low had indeed intensified and moved southward of its climatological mean position. The January 1983 map of sea level amospheric pressure in the Gulf of Alaska (Fig. 21) is qualitatively similar to the central part of the bottom of Fig. 20. The surface winds implied by the low-pressure pattern in Fig. 21 drive near-surface ocean currents approximately parallel to the pressure contours, in a cyclonic direction, as indicated by the drogued buoy tracks.

The anomalous winter 1983 atmospheric circulation also produced anomalous wind-driven transports which helped to create the SST anomalies observed during winter–spring in the Gulf of Alaska (Wagner 1984; Simpson 1985). For example, the anomalous southward transport in the western part of the Gulf of Alaska (as implied by Fig. 21) brought cold water from the north into the central North Pacific. This mechanism probably helped produce the cold SST anomaly in this region during

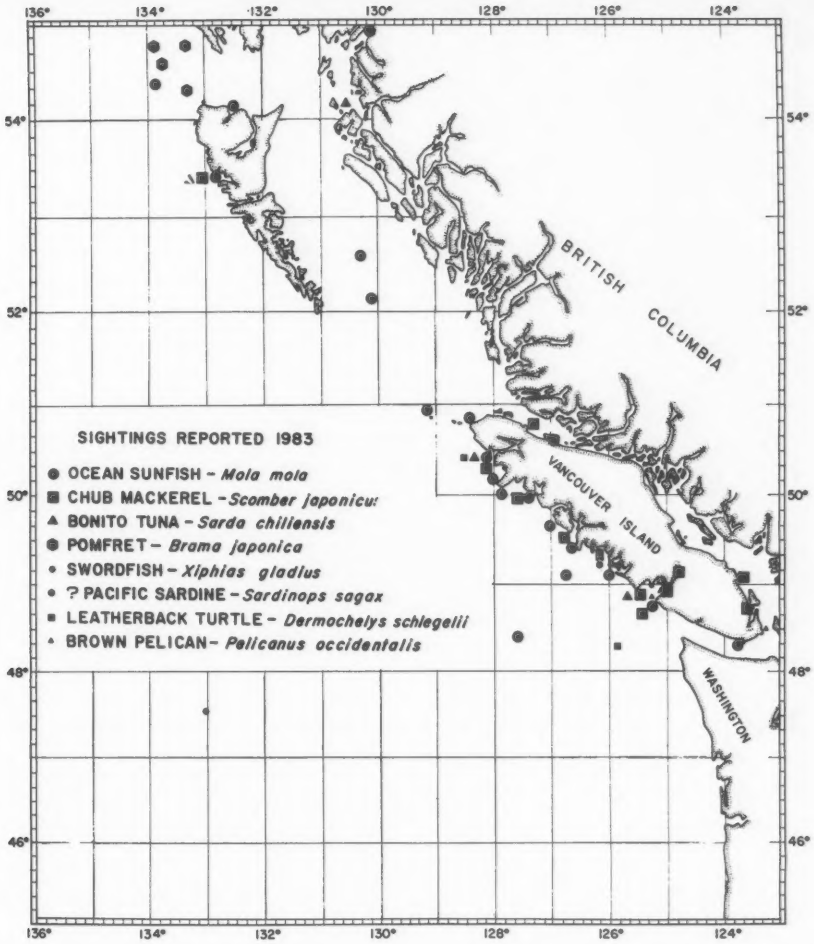


FIG. 28. Distribution of exotic species seen off British Columbia during 1983 (courtesy of J. Fulton, Pacific Biological Station, Nanaimo, B.C.).

winter–spring 1983 (Fig. 19b, 19c). An additional contribution to the cold anomaly may have come from enhanced local mixing of the surface water with the colder subsurface water, a process caused by the increased storm activity near the center of an intensified low (Haney et al. 1983). Ekman pumping (open-ocean upwelling) is a third mechanism which can help to produce a cold SST anomaly in the center of an intensified low-pressure system.

The anomalous winter 1983 atmospheric circulation also produced enhanced eastward transport towards the California coast (J. J. Simpson, pers. comm.). This brought in the observed low-salinity Pacific Subarctic water, and caused high sea surface and subsurface temperatures, a depressed thermocline, and high sea levels, although the rise in the latter during fall (and the concomitant strengthening of the inshore California Counter Current) was largely due to the lower than normal pressure over central California (Fig. 20, top). During winter and spring of 1983 the storm tracks associated with the prevailing westerlies moved southward because of the expanded Aleutian low and caused increased rainfall and severe flooding in most of California.

The anomalous atmospheric winter conditions just described also occurred over the North Pacific during 1941 and 1958 (e.g. see Fig. 26a) and hence caused, during these ENSO years, the high sea levels noted in Fig. 1 and 17, the warm SST depicted in Fig. 3, 4, and 18, and the low pressure and high rainfall seen in Fig. 5. The relationships between the winter sea level atmospheric pressure and the ocean conditions in the North Pacific since the Second World War have been investigated by Davis (1976) and by Emery and Hamilton (1985). The relationship between the 700 mb pressure anomalies and the SST anomalies has been studied by Namais and Born (1972).

Because of the intensified Aleutian low, the surface winds along the British Columbia coast during winter and spring 1983 were generally very strong from the southeast. This produced anomalous onshore transports of warm water from the south and southwest (as implied by the drogue tracks in Fig. 21) and led to a longer than normal period of downwelling over the shelf (Fig. 22). Also, such transports would have tended to

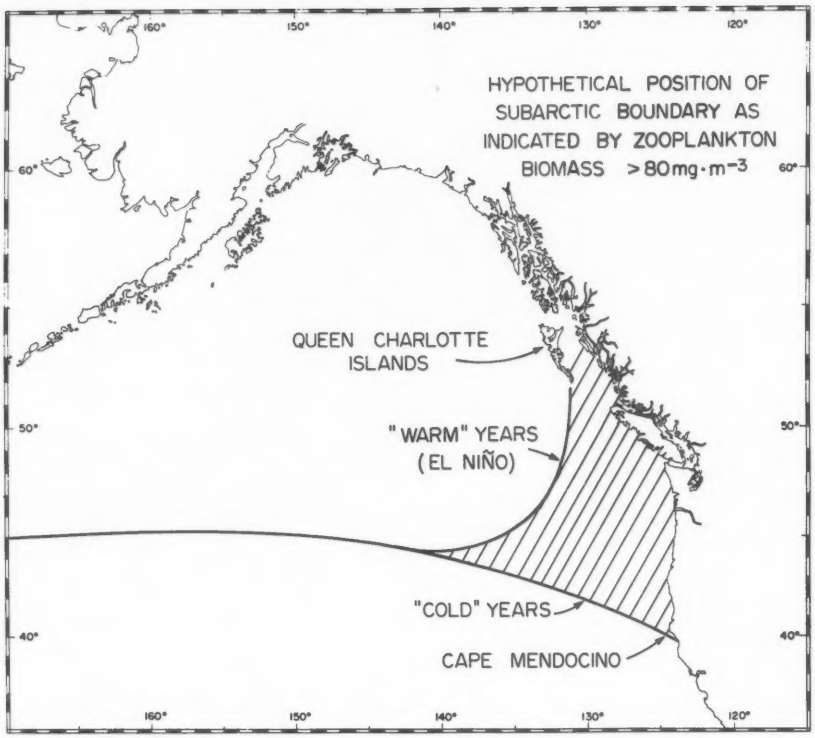


FIG. 29. Schematic diagram of the area affected by shifting of subarctic boundary (Fulton and LeBrasseur 1985).

keep dilute (low-salinity) water near the coast. Normally, by spring the winds along the Oregon – British Columbia coast have switched over to being northerly and hence upwelling favorable (Fig. 23). The high coastal sea levels (caused mainly by onshore transports and low atmospheric pressure) and strong southerly winds along the inner shelf produced narrow, intensified northward warm currents near the shore (i.e. an enhanced Davidson Current). These currents were fortuitously detected along the Oregon – British Columbia and Alaskan coasts during January–March 1983 with satellite-tracked buoys (see fig. 6 in Emery et al. 1985). The average speed of these currents was about 30 $km \cdot d^{-1}$, although daily speeds of nearly 100 $km \cdot d^{-1}$ were sometimes recorded.

The PNA teleconnection pattern is only one of several such structures in the atmosphere. Figure 24 and Table 2 define four Northern Hemisphere winter teleconnection patterns in other parts of the world which have been identified by Wallace and Gutzler (1981) and investigated further by Blackmon et al. (1984). Some of these patterns may be excited during major ENSO episodes and hence could account for wide-ranging climatic anomalies in the Northern Hemisphere, which in turn could affect the fisheries in oceans other than the Pacific.

Local Atmospheric Forcing of Northeast Pacific Warmings

Several authors who discuss possible El Niño impacts on fisheries in the northeast Pacific tacitly assume, incorrectly, that each tropical ENSO event produces a noticeable signal in the northeast Pacific Ocean (e.g. a positive SST anomaly). They did not generally recognize that a warm SST anomaly off the British Columbia – Alaska coast can occur during a year in which there is no ENSO episode in the tropics. Thus, to suggest that ENSO episodes will generally produce biological changes in the northeast Pacific Ocean such as those illustrated in Fig. 28 and 29 can be very misleading. The most reliable way to infer the presence of warm SST anomalies and anomalous currents in the northeast Pacific (and hence to determine the possible biological impacts) seems to be by an examination of the winter sea level atmospheric pressure maps (Wagner 1984; Emery and Hamilton 1985; Simpson 1985).

The strong ENSO events of 1957–58 and 1982–83 both produced anomalous warmings off the west coast of North America during winter–spring of 1958 and 1983 in a manner consistent with the teleconnection mechanism described above. Comparison of Fig. 25 with Fig. 26a (top) reveals that during winter of 1958 the Aleutian low intensified and expanded to the east. In response to this anomalous low-pressure system (five closed contours as compared with the climatological three in Fig. 25), there was above-average northward advection of warm water along the west coast of North America (Tully et al. 1960); in addition, because of the northward shift of the surface thermal structure during a major ENSO event (Emery and Hamilton 1985), the warm water advected northward is anomalously warm in its origin. Hence, the resultant SST anomaly pattern shows a wide band of warm water off the west coast, extending outward a distance of about 2000 km. The cold SST

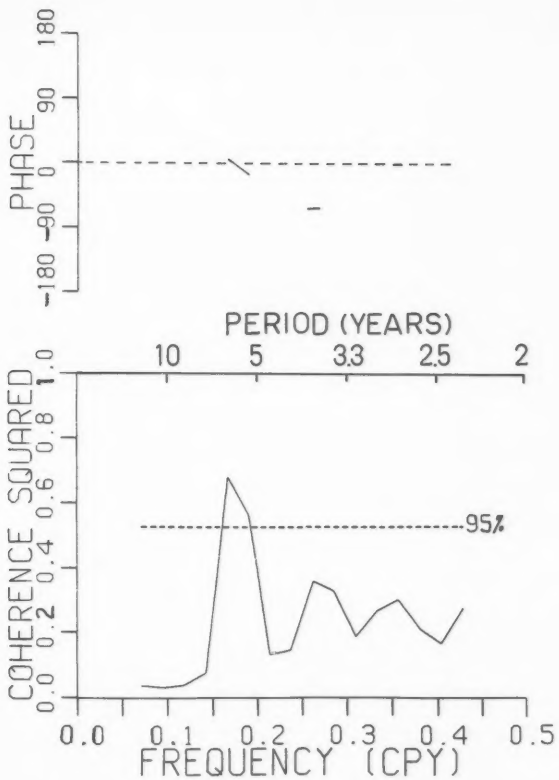


FIG. 30. Cross-spectrum between herring recruitment on the west coast of Vancouver Island and mean annual salinity at Amphitrite Point, British Columbia, for the period 1935–76 (MHP). The phase is in degrees and is positive when the second time series leads the first.

anomaly farther to the west presumably resulted from anomalous local mixing, open-ocean upwelling, and advection of cold water from the northwest Pacific.

Bjerknes (1966) and Namais (1976) noted that during winter of 1957, the atmospheric circulation in the North Pacific was anomalously weak (similar to that in Fig. 26c, top). The same situation also occurred during winter of 1982. Emery and Hamilton (1985) have suggested that during the winter prior to a major ENSO event (which results in a significant warming off the west coast of North America during the next winter), the North Pacific atmospheric circulation will generally be weak, and that this pattern will be followed by an intensified expanded Aleutian low during the next winter.

Figure 26b (bottom) shows the occurrence of a warming off the coast in a year (1961) in which there was no tropical ENSO event. The appearance of the large cold SST anomaly in the central North Pacific and the band of warm water along the California – British Columbia coast is respectively due to anomalous upwelling and advection caused by the intensified and expanded Aleutian low (Fig. 26b, top). The occurrence of relatively weak positive SST anomalies occupying a smaller region during 1961 as compared with 1958 is probably due to the absence of a strong tropical El Niño.

Figure 26c (top) shows a weaker than normal circulation during winter 1972, with the Aleutian low broken into two parts. The corresponding SST anomaly pattern (Fig. 26c, bottom) contains a relatively warm region in the central North Pacific but cold SST's along the west coast. Although the 1972–73 ENSO event has been described as strong in terms of its tropical behavior, the normal PNA teleconnection pattern did not develop in winter of 1973. Rather than an intensified and expanded Aleutian low forming in winter of 1973, the circulation approached normal conditions (Fig. 26d, top). Consequently, the 1973 winter SST anomaly pattern (Fig. 26d, bottom) was similar to that for winter of 1972, although the intensity of both the cold and warm anomalies decreased by a factor of two or more.

As a final example, the rather unusual situation for winter of 1977 is shown in Fig. 26e. The 1976 ENSO event has been described as moderate (Table 1), yet the intensity of the Aleutian low was the strongest for the 36-yr period studied by Emery and Hamilton (1985). Accordingly, the warming off the west coast was extensive, with maximum SST's comparable with the 1958 warming. Also, the region of the central cold anomaly expanded far to the west.

Table 3 summarizes the results of the above case studies, and also serves to emphasize the close relationship between the strength of the North Pacific winter sea level atmospheric circulation and the SST's in the northeastern Pacific. An unabridged version of this table for the period 1947–83 is given in Emery and Hamilton (1985). A convenient way if displaying the strength of the atmospheric circulation during winter is to plot, as a function of year, the North Pacific atmospheric pressure index (Emery and Hamilton 1985), defined as the sea level pressure in California minus that in the Gulf of Alaska (see also Fig. 25). High and low values of this index correspond to strong and weak circulations, respectively; moreover, the SST fluctuations along the coast closely follow the index changes (Fig. 27) in agreement with the pattern seen in Fig. 26. The strong correlation in the two time series shown in Fig. 27 (the correlation coefficient is 0.73) indicates that to a high degree of accuracy, sea level atmospheric pressure data can be used to produce synthetic coastal temperature data during years in which no such measurements were made.

Impact on Fisheries

The physical environmental variables which are believed (Wooster 1983a; McLain and Thomas 1983; Pearcy 1984) to have a significant impact on fish survival, growth, and migration timing and routes in the northeast Pacific are water temperature, salinity, currents, and parametric measures of stability, turbulence, and turbidity (e.g. the square of the Brunt–Väisälä frequency must be positive for static stability, see LeBlond and Mysak (1978, p. 15)). Important biotic factors which affect fish abundance and migration are availability of food (and the competition for it) and predation. Year-to-year variations of the latter factors can partly be caused by the changes in the oceanic variables, which we have seen are often generated by interannual fluctuations in the atmosphere.

In the hope of stimulating further research on ocean–fish interaction studies, I now give some examples of how interannual changes in temperature, salinity, and current in the northeast Pacific Ocean appear to be related to interannual variability in the regional fisheries. For a discussion of the effects of changes in turbulence and vertical stability on spawning and fish survival in the California Current system, see Husby and Nelson (1982).

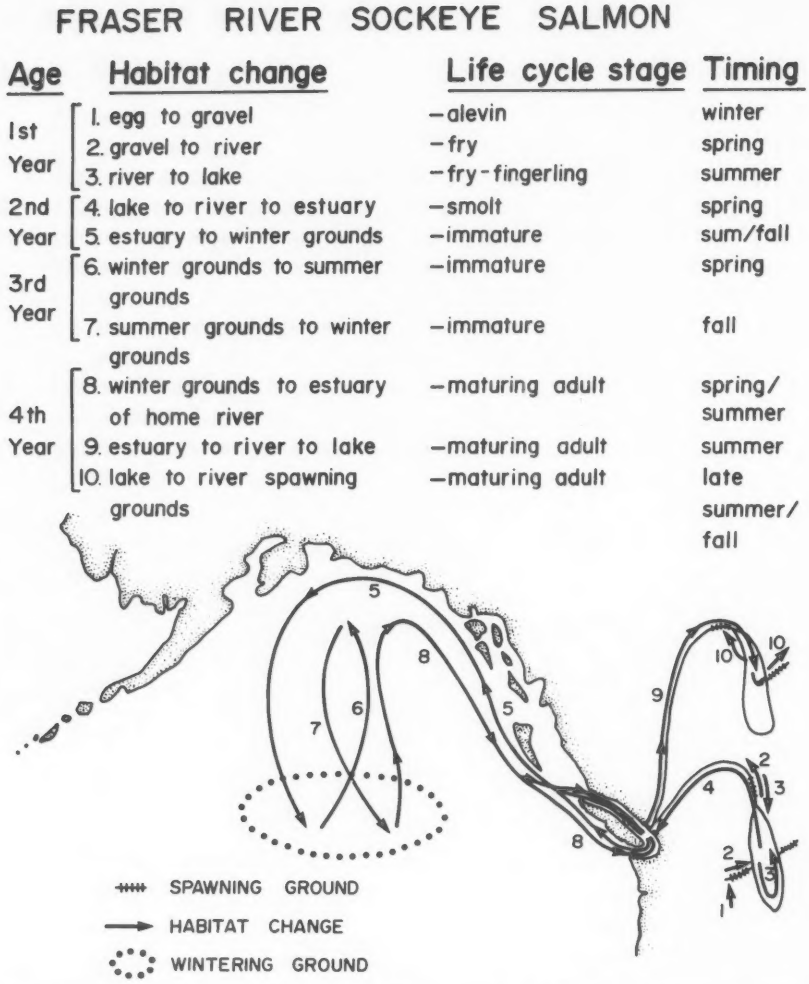


FIG. 31. Habitat changes (migration routes) of sockeye salmon of the Fraser River system during their 4-yr life cycle (Groot et al. 1984).

Distribution of Exotic Species and Zooplankton during an ENSO Event

Because of the greatly expanded and intensified Aleutian low during winter of 1983, there were anomalous transports of warm water toward the British Columbia coast from the south and southwest. Consequently, many exotic warmwater species of fish, birds, and turtles were sighted (J. Fulton, Pacific Biological Station, Nanaimo, B.C., pers. comm.) off the British Columbia coast during spring–summer of 1983 (Fig. 28). What is perhaps most remarkable is that a number of these species (e.g. chub mackerel (*Scomber japonicus*), ocean sunfish (*Mola mola*)) were also seen in the inshore waters (Strait of Georgia, Hecate Strait), a feature which illustrates the tremendous strength of the 1982–83 ENSO event. During 1958, the second year of the major 1957–58 ENSO event, several subtropical fish species were also observed at unusually high latitudes (Radovich 1961), and the British Columbia catch of whales was extremely anomalous (e.g. the finback whale (*Balaenoptera physalus*) catch was over three times the previous 6-yr average (Tully et al. 1960)).

Fulton and LeBrasseur (1985), using the data base of LeBrasseur (1965), have investigated the effects of interannual variations in ocean circulation on zooplankton biomass distribution in the northeast Pacific during the period 1956–63. During "normal" or "cold" years the subarctic boundary, which divides the Alaskan gyre from the California Current system, extends approximately east–west across the eastern Pacific (Fig. 29). To the north of this boundary, the zooplankton community is dominated by larger copepods, resulting in a biomass density >80 mg·m^{-3}. However, during ENSO years, such as 1958, the subarctic boundary shifts northward along the coast (Fig. 29) and the biomass density off Vancouver Island is decreased. Fulton and LeBrasseur (1985) speculated that this decrease would cause reduced growth, and, possibly, reduced survival of juvenile salmonids in the hatched region in Fig. 29.

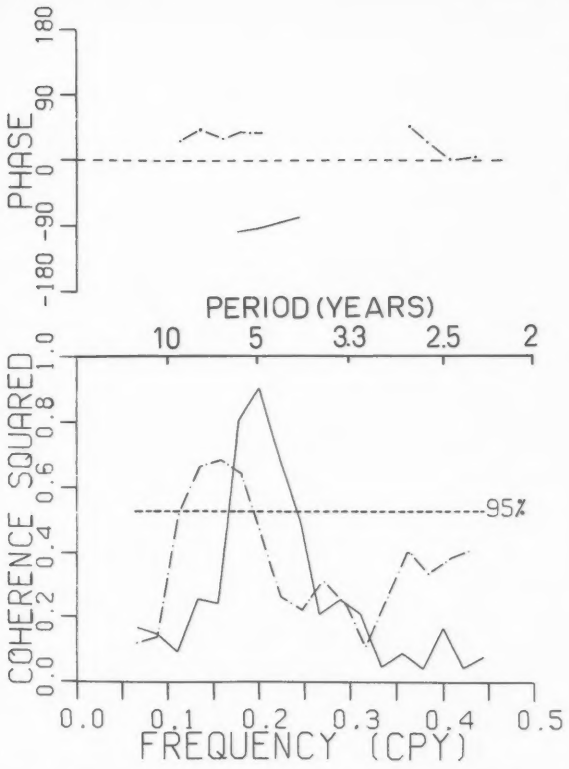


FIG. 32. Cross-spectra between normalized weight anomaly of Fraser River sockeye, *w*, and temperature at Amphitrite Point (solid line), and between the number of sockeye caught in Convention waters, *N*, and temperature at Amphitrite Point (dot-dashed line) (MHP). The phase is in degrees and is positive when the second time series leads the first. The time series used to compute the spectra covers the period 1934–77.

Impact on Selected Nonsalmonid Species

The relationship between ENSO episodes and the migration patterns of the bluefin tuna (*Thunuus thynnus*) in the Pacific Ocean was investigated by Yamanaka (1984). During normal years (or years of weak ENSO events), the juveniles migrate eastward (roughly along 40°N) across the North Pacific as far as California, return westward along 20°S, and spawn near Japan. The postspawners then traverse a large transequatorial, clockwise loop in the western Pacific, which extends southward as far as New Zealand. During strong (2-yr) ENSO episodes, the east–west migratory loop shifts southward about 10–15°, presumably in response to the large cold SST anomaly which develops during the second winter in the central North Pacific. Also, in keeping with their preference for warmer water, the postspawners during strong ENSO years tend to be found farther to the east in the South Pacific; in particular, some migrate as far east as Peru and Chile.

The Pacific whiting (*Merluccius productus*), the target of a large foreign fishery since the mid-1960's, follow a migratory pattern which extends over 2000 km along the west coast of North America (Francis and Bailey 1983). The fish spawn during winter off Baja California, travel northward along the shelf during spring, reach their feeding grounds off Vancouver Island in summer, and then return southward during fall along the outer continental slope to their winter spawning grounds. During the spawning, nursery, and juvenile life stages, changes in the offshore water temperature and circulation pattern could significantly affect their survival and growth. Since both the temperature and currents along the west coast change from year to year, interannual variations in stock abundance (and perhaps migration timing) would be expected. However, to date, such fish–environment interactions have not been studied seriously, especially with a view toward connections with ENSO episodes. Some of the interactions which deserve further study follow. First, Pacific whiting are known to spawn in the deep slope waters off Baja California (probably in the northward flowing California Undercurrent), but their exact location appears to be determined by the subsurface temperature, with more northerly spawning occurring during years of anomalous subsurface warming (as in 1983). Does this consistently happen during strong ENSO episodes which warm the California coastal waters? Second, since the nursery is located inshore, over the shallow shelf waters, anomalous onshore advection (Ekman transport) would appear to enhance their survival (Francis and Bailey 1983). Is there any evidence of a correlation between year-class strength and ENSO episodes during which such anomalous onshore transports tend to occur? Third, during the northward migration of the juveniles in spring, the presence of anomalous northward shelf currents (the Davidson Current) would presumably help the young fish reach their summer feeding grounds sooner and hence contribute toward their survival and growth. Can such a hypothesis be tested? Finally, it is speculated that the timing of the return migration may depend on the local oceanic conditions off Vancouver Island, which of course also vary significantly from year to year.

Tyler (1983) noted that during the past 30 yr, significant fluctuations have occurred in year-class strength of Hecate Strait English sole (*Parophrys vetulus*) and rock sole (*Lepidopsetta bilineata*). In particular, strong year-classes were observed for both species throughout 1953–55, 1961–62, and 1969–70. In several of the intervening years, poor survival was noted, especially for 1957, 1958, 1964–66, and 1971–73. Since these latter periods roughly correspond to strong or moderate El Niño event years (Table 1), Tyler (1983) speculated that El Niño (because of associated warm water temperatures) has an influence on sole survival. However, in the absence of any proposed mechanisms it is difficult to comprehend such a relationship. Apart from the very anomalous 1958 warming, the coastal temperature during the high-survival years (1953–55, 1961–62, and 1969–70) tended to be near normal as was also the case during the poor survival years 1957 and 1964–66 (see Fig. 27 and 35). And in 1971–73, the water off the British Columbia coast was anomalously cold, which should, according to the speculated relationship, have produced a strong year-class. However, just the opposite occurred. This example shows that it is misleading to blame El Niño for poor survival without a careful look at local conditions.

Pearcy (1983) has recently enumerated a number of abiotic environmental variations which may produce the large interannual fluctuations that are observed in Pacific herring (*Clupea harengus pallasi*) recruitment and year-class strength (e.g. see MHP, fig. 18; Pearcy 1983, fig. 1). These range from individual storms and freshets which would affect survival of cohorts

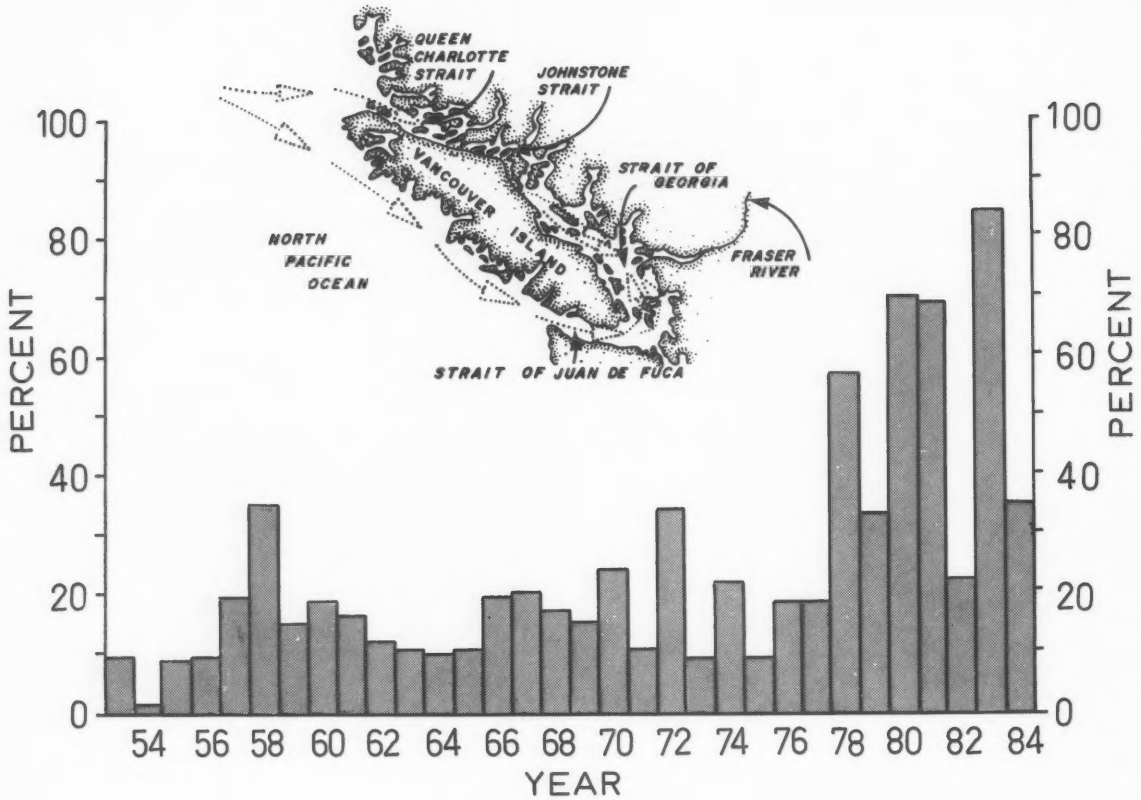


FIG. 33. Inset: migratory routes of adult sockeye salmon on their way to the Fraser River and other southern British Columbia and Washington State spawning grounds. Histogram: percentage of sockeye salmon approaching the Fraser River through the northern passage during 1953–84 (the so-called Johnstone Strait diversion). (Figure adapted from Groot et al. (1984)).

in an inlet to large-scale interannual events such as ENSO which cause changes in the circulation and food production in the Gulf of Alaska.

One notable, apparently environmentally induced change in year-class strength occurred in the period 1957–65. Strong 1957–59 year-classes in the Bering Sea and southeastern Alaska herring were followed by weak year-classes in the 1960's. A similar trend also occurred for the British Columbia herring, and Wickett (1975) noted that this pattern roughly coincides with the salinity changes at Station P (50°N, 145°W) during this period: salinities were relatively high during 1958–61 and relatively low during the 1960s. According to Wickett (1975), high survival occurred during times of high salinity because the latter can be regarded as a measure of winter storm mixing of the water column which caused upward movements of nutrients into the euphotic zone, and thus, a tendency toward increased production (see also Fulton (1983) regarding similar zooplankton biomass changes at Station P). Over a longer period (1935–76), MHP also found a strong in-phase correlation between salinity (S) and herring recruitment on the west coast of Vancouver Island. The cross-spectrum (the correlation as a function of frequency) between S and herring recruitment is significantly peaked at a period of about 6 yr, indicating a strong coupling between the two variables (Fig. 30). This may be due to the fact that following a winter of high S (stormy conditions), there is a longer spring phytoplankton bloom which is better for the zooplankton growth and hence herring survival (T. R. Parsons, Department of Oceanography, University of British Columbia, Vancouver, B.C., pers. comm.).

In addition to the strong year-classes in the late 1950's, which coincide with the strong 1957–58 ENSO episode, Pearcy (1983) noted that southeastern Alaska herring had large year-classes in other strong or moderate El Niño years, namely 1926, 1929, 1939, 1951, and 1953. Since a number of these years correspond to anomalously warm years (Fig. 27 and 35), a relationship with temperature is suggestive. However, MHP found no significant correlation between SST and herring recruitment in northern British Columbia or west Vancouver Island, which indicates that the effect of interannual abiotic changes is complex. However, one promising avenue of research is to study the relationship between recruitment and advection (M. Sinclair, Department of Fisheries and Oceans, Halifax, N.S., pers. comm.). Anomalous coastal currents will be associated with anomalous sea levels, and indeed, MHP (see their fig. 13) found a significant peak at 6 yr in the cross-spectrum between Ketchikan sea level and northern British Columbia herring recruitment. Moreover, the data show that sea level leads recruitment by about 1 yr, indicating that survival depends strongly on ocean conditions at the larval stage.

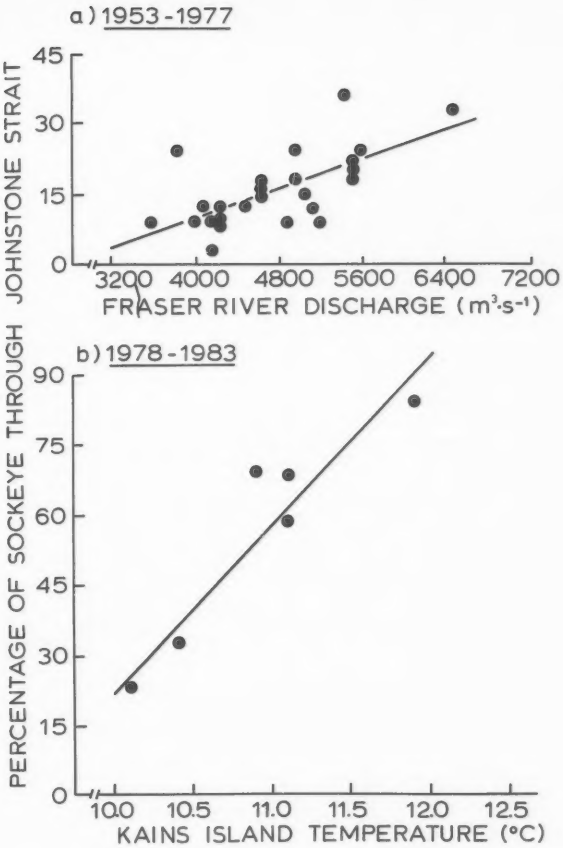


FIG. 34. (a) Linear regression of the Johnstone Strait diversion of the Fraser River sockeye during 1953–77 on the Fraser River discharge (averaged over April–June). The correlation coefficient is 0.68. (Courtesy of C. Groot and T. Quinn, Pacific Biological Station, Nanaimo, B.C.) (b) Linear regression of the Johnstone Strait diversion of the Fraser River sockeye during 1978–83 on temperature (average over April–June) at Kains Island (see Fig. 18c). The correlation coefficient is 0.93. (Courtesy of C. Groot and T. Quinn). From this regression, Groot predicted about a 36–37% return through Johnstone Strait during 1984. The unofficial return rate at the time of writing is 35% (D. Blackbourn, International Pacific Salmon Fisheries Commission, New Westminster, B.C.).

Another indication of the importance of coastal currents (as measured by sea level) on fish survival has been given by Sinclair et al. (1985). They found an essentially one-to-one relationship between the interannual variability in survival of Pacific mackerel to age 1 and the sea level off southern California. Good survival is associated with high sea level (i.e. reduced southward flow of the California Current). Poor survival is associated with strong southward flow. Thus, ENSO events, which produce high sea level along the California coast, generate conditions which are beneficial for the survival of Pacific mackerel.

Impact on the Sockeye Salmon

Because of the great economic importance of the sockeye salmon fishery in Alaska and British Columbia, considerable effort has been devoted to the study of the influence of oceanic variability on sockeye abundance, return migration timing, and routes. Rogers (1984) reviewed the trends in abundance since the 1900's in western and central Alaska and noted that major changes in abundance appear to be associated with air and water temperature variations, especially during winter months. Tabata (1984c) discussed the various oceanographic conditions that influence the distribution, migration, and survival of the Fraser River sockeye salmon.

In a study of Bristol Bay sockeye salmon migration routes and timing, Burgner (1980) found that the return time of the salmon (in May–June) to a coastal fishery is correlated with SST. In years when the water is warmer, the salmon generally arrive earlier than in cooler years. Conceivably this response to the environment occurs because at this time of year, the sockeye in the North Pacific have a fairly small preference range of temperature, about 5–7° (Tabata 1984c, table 1). Since the range of interannual temperature changes extends beyond this, year-to-year fluctuations in the return time would be expected. During anomalously cold years, the salmon may have moved farther south to find their preferred temperature range and hence would take longer to swim back to their spawning grounds than in warmer years. Long-term SST changes also appear to affect the abundance of the Bristol Bay sockeye in the North Pacific (Rogers 1984). During cold years when the salmon are farther south, they may become more concentrated and hence more vulnerable to predators. This may have occurred during the period 1950–75, when the salmon catch steadily declined while also a gradual cooling trend in the ocean occurred (Chelton 1984, fig. 3). Conversely, following a steady warming trend which began around 1976 (Chelton 1984; McLain 1984; see also Fig. 35), the abundance has steadily increased. However, an additional factor which has lead to the resurgence of the Bristol Bay sockeye is the reduced high seas interception of the returning salmon by fishermen (Eggers et al. 1984).

During most major ENSO years or the year after, the total British Columbia sockeye salmon catch (landed weight) was relatively large (Fig. 6). Recently M. C. Healey (Pacific Biological Station, Nanaimo, B.C., pers. comm.) found a similar pattern in the number of British Columbia sockeye caught each year. However, peaks in the British Columbia catches also occurred in other years in which there were marked local warmings (e.g. 1953 and 1977, see Figs. 4 and 6) but no strong ENSO episodes (Table 1). Part of these increases in catch may be due to strong runs associated with the 4-yr cycle of a few particular stocks[3] (the sum of which make up the total British Columbia sockeye salmon population). Thus, ideally, one should attempt to remove this population-specific variability before discussing possible ENSO or local warming influences. Even allowing for this caveat, however, it is remarkable that during the local warming of 1958 (an example of a typical response to the strong 1957–58 ENSO event), the high catch shown in Fig. 6 coincided with an anomalously high zooplankton biomass distribution to the northwest of Queen Charlotte Sound during late spring of 1958 (see fig. 4 in Fulton and LeBrasseur 1985). If this also produced an increase in the food supply (small fish, squid, etc.) for the mature sockeye salmon which returned to their spawning rivers via this region during spring–summer (e.g. see route 8 in Fig. 31), then an increase

[3]The largest single stock of all the Fraser River stocks is popularly called the "Adams River Rum," which had peaks in 1942, 1946, etc.

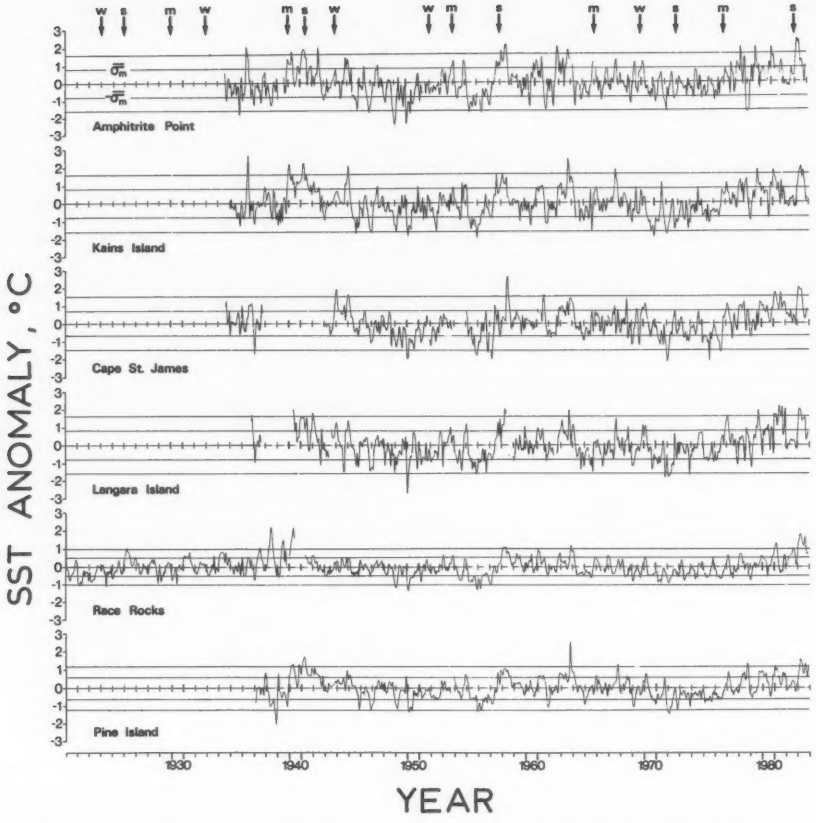


FIG. 35. Monthly SST anomaly records at six monitoring stations along the British Columbia coast (see Fig. 18c). Horizontal lines represent one and two times the annual mean of the standard deviation for each month ($\bar{\sigma}_m$). Arrows denote occurrence of weak (w), moderate (m), and strong (s) ENSO events as given in Table 1. (Courtesy of R. E. Thomson, Institute of Ocean Sciences, Sidney, B.C.)

in the size of the salmon during this anomalously warm year may be expected. However, it is also important to note that 1958 was also an "on year" for the Adams River Run, and hence the large 1958 catch shown in Fig. 6 may be partly due to this purely population-specific feature.

Additional evidence of this relationship (large catch in warm years) is indicated by the significant 7-yr peak in the dot–dashed line in the lower part of Fig. 32, which represents the coherence squared between the number (N) of Fraser River sockeye salmon caught in conventional waters and the temperature (T) at Amphitrite Point. Since the phase (upper part of Fig. 32) is not significantly different from zero at the 7-yr peak, this cross-spectrum indicates that the temperature and population fluctuations are approximately in phase and have a 7-yr cycle.

A different relationship exists between the Amphitrite Point temperature fluctuations and the Fraser River sockeye weight anomaly w, defined as $w = (W - Y)/Y$, where W = average weight per fish in a given year and Y = average weight of the particular cycle-class to which W belongs (e.g. Y for the 1915 year-class is calculated by averaging the values of W for 1915, 1919, 1923, etc.). The time series for w is thus a filtered series in which the biological-specific 4-yr cycle of these sockeye is eliminated.

The coherence squared between w and T at Amphitrite Point (solid line in Fig. 32) shows a large peak at 5 yr. Moreover, the phase of $-90°$ at this peak implies that the temperature fluctuations lead those of w by 3.75 yr. Since the Fraser River sockeye are a 4-yr cycle fish, this lead means that an increase (decrease) in temperature affects the sockeye near the beginning of its life cycle (e.g. as an alevin) in a manner which results in heavier (lighter) fish near the end of its life cycle. One way this might happen is that warmer water aids the incubation of some stocks and thus produces heavier than normal young fish. Also, during warmer years, the rainfall in the Fraser River drainage system is above normal. Perhaps this leads to an above normal food supply which helps the very young fish grow more rapidly, the final result being a heavier fish just before spawning time.

By way of contrast, Rogers (1980) found that temperature fluctuations have a relatively small effect on the interannual weight variations of 6-yr-old Bristol Bay sockeye. He showed that the weight changes depend mainly on the initial density of fish: during years of high (low) density, the growth rates are small (large) and hence the mature fish weights are small (large).

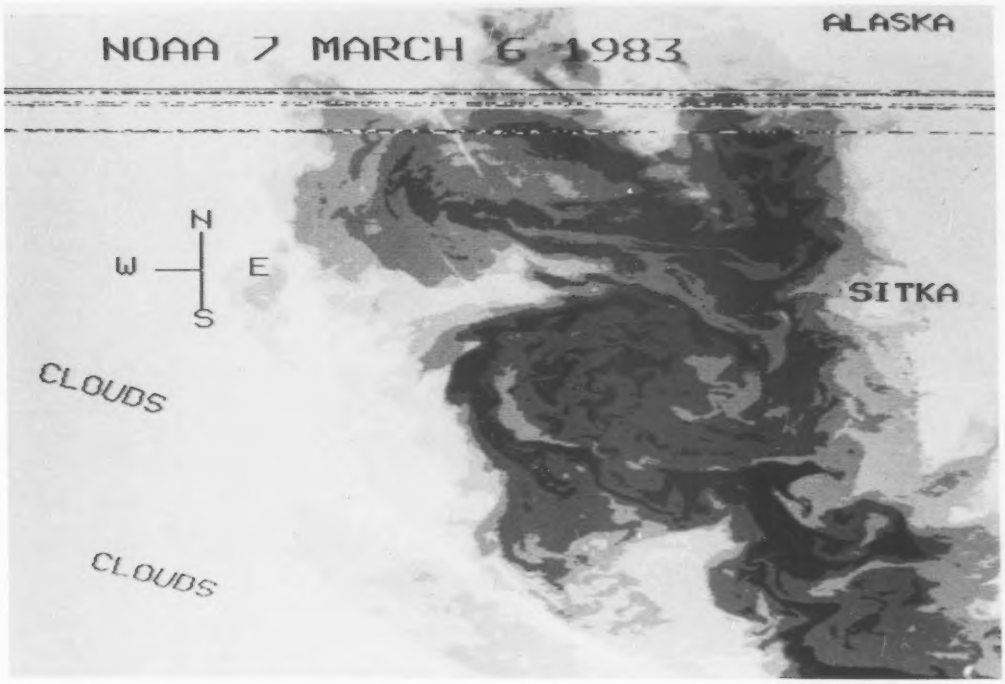


FIG. 36. Thermal infrared satellite image of the clockwise-rotating Sitka eddy (centered at approximately 57°N, 139°W), 6 March 1983. Dark shades correspond to warm water and light shades to cold water, with the maximum temperature contrast being about 1°C. (Courtesy of A. Thomas, Department of Oceanography, University of British Columbia, Vancouver, B.C.) Note the ribbon of cold offshore water being drawn in toward the coast on the northern side of the eddy.

The Fraser River sockeye salmon can take either a northern or a southern route around Vancouver Island during their homing migration in summer (see Fig. 31 and inset at top of Fig. 33). During the past 31 yr the percentage of sockeye taking the northern route (which I shall call the "Johnstone Strait diversion") has varied from 2 to 85% (Fig. 33), with the maximum value occurring in summer of 1983, just after the very strong 1982–83 ENSO episode. The wide-ranging fluctuations in the return route have created considerable problems in the management of the sockeye fishery in southern British Columbia. Thus, it is important to find the mechanisms that produce these remarkable fluctuations. One ongoing study (Groot et al. 1984) is testing the hypothesis that the mature salmon return along the route that they used (and "memorized") as young juveniles enroute to the open ocean 2 yr earlier. However, the bulk of the earlier literature on this topic deals with the possible influence of the oceanic conditions on the route taken by the returning salmon.

Because the relatively large 1958 diversion (35%) occurred during the second year of the strong 1957–58 ENSO episode, it was proposed by Tully et al. (1960) and Royal and Tully (1961) that the change in migration route for many of the sockeye salmon was a direct consequence of the warm water intrusion from the south. Rather than making landfall on the west coast of Vancouver Island and then migrating south along the outer coast to the entrance of Juan de Fuca Strait, many of the fish, being farther north than usual, made landfall north of Vancouver Island and then migrated south through the inland waterways and thus eventually passed through Johnstone Strait.[4] However, this proposed mechanism did not explain the next relatively large diversion in 1972 because during that year the local waters were anomalously cold (see Fig. 3, 26c, and 35).

Favorite (1961) and Wickett (1977), on the other hand, took the view that the relatively high Johnstone Strait diversions that occurred in some of the years prior to 1977 may be related to the presence of anomalously low-salinity tongues (making up the so-called dilute domain) that emanated seaward from Queen Charlotte Sound and which the returning sockeye may be trying to find as they migrate southward along the coast. Such relatively fresh water could be produced by higher than normal discharge from the Fraser River (and other neighboring rivers) during spring. According to P. Crean (Department of Oceanography, University of B.C., Vancouver, B.C., pers. comm.), the Fraser River plume can sometimes extend well into the northern end of the Strait of Georgia and beyond. Indeed, in support of the Favorite–Wickett hypothesis, C. Groot and T. Quinn (Pacific Biological Station, Nanaimo, B.C., pers. comm.) have shown that for the period 1953–77, the Johnstone Strait diversion is highly correlated with the springtime Fraser River discharge (Fig. 34a). The period analyzed by Groot and Quinn roughly coincides with that of a long-term cooling trend in the northeast Pacific which began in

[4]This tacitly assumes that as a homing migration mechanism, the salmon in the open ocean head straight to the coast, turn right when reaching there, and then search for the first major opening (e.g. Juan de Fuca Strait).

the late 1950's (Chelton 1984). Because this trend is toward the colder water temperatures generally preferred by the mature salmon, it is perhaps not surprising that salinity (as opposed to temperature) anomalies have played a more important role in determining the Johnstone Strait diversion up to 1977. However, after 1977 a new regime of relatively high diversions occurred (average = 53% for 1978–84; range = 23–85%). Further, Fig. 34b shows that these anomalous diversions are very highly correlated with the temperature variations at the northern end of Vancouver Island, which is consistent with the findings of IPSFC (1984). Also, the period of this new regime coincides with a significant warming trend in the northeast Pacific (Chelton 1984; McLain 1984) which began in 1977; this trend is also clearly visible in the SST records from various British Columbia coastal monitoring stations (see Fig. 35). Surface salinity anomalies may have been less important in determining the diversion during the past 7 yr because with the occurrence of high water temperatures, the salmon have been observed to return at deeper levels (C. Groot, Pacific Biological Station, Nanaimo, B.C., pers. comm.), and thus are out of the range of near-surface influences.

Hamilton (1985) used commercial catch data to find the Johnstone Strait diversion percentages for the period 1906–52. Using the extended time series (1906–83), he was able to show that there is at most a weak relationship between the Johnstone Strait diversion and the 4-yr cycle of the sockeye. However, there is a strong correlation between the northern diversion percent and the duration of the spawning run: during years of relatively high diversion, the run tends to be spread out over a longer period. Also, Hamilton (1985) found a very strong correlation between the diversion percentage and the temperature change in coastal waters off Vancouver Island over the last 18 mo of the salmon's ocean residence.

In addition to temperature and salinity changes, interannual variations in the near-surface circulation pattern of the northeast Pacific could also affect the timing and location of the return migrations. Such circulation changes would include shifts in the positions of the main Alaskan gyre and related frontal systems (Royce et al. 1968) and the production, propagation, and dissipation of eddies off the British Columbia – Alaska coast (Tabata 1982; Swaters and Mysak 1985; Mysak 1985). A particularly notable eddy which is likely to change sockeye migrations from year to year is that which occurs intermittently to the west of Sitka, Alaska (57°N, 135°W), colloquially known as the "Sitka eddy" (Tabata 1982; see also Fig. 36). This is a large (diameter~300 km), clockwise-rotating, warm-core eddy which is believed to be generated in spring–summer by the interaction of the northward-flowing coastal current (the Alaska Current) with bottom topography (Swaters and Mysak 1985). However, its occurrence appears to be closely tied in with the nature of the preceding winter atmospheric circulation, which controls the strength of the upstream coastal current. In particular, Swaters and Mysak (1985) noted that the eddy is generated just after the relaxation of an intensified and expanded wintertime Aleutian low, a phenomenon which occurred, for example, in 1958, 1977, and 1983. Since the axial currents (associated with the Sitka eddy are on the order of 0.5–1.0 $m \cdot s^{-1}$, they appear to significantly affect the migration route of the returning sockeye because the latter swim at comparable speeds. In a study of this fish–eddy interaction problem using catch data for the period 1952–62, Hamilton and Mysak (1986) found that in years when the Sitka eddy is present the spawning migration routes of the salmon returning to the Nass and Skeena rivers tend to be deflected to the south. An analysis of salmon tagging data collected during 1957 (when the eddy was absent) and 1958 (when the eddy was present) supports this conclusion. The southward deflection during 1958 is a particularly striking result in light of many other observations (e.g. Radovich 1961) which show that several fish species were displaced northward during the 1958 warming of the northeast Pacific.

Discussion

From an in-depth discussion of ENSO events and their impact at higher latitudes, I have shown that local warmings and anomalous currents in the northeast Pacific cannot simply be determined from a catalogue of ENSO years (Table 1). Rather, one should examine the strength of the winter atmospheric circulation associated with the Aleutian low. When the North Pacific circulation is strong (weak), the winter mean SST along the west coast of North America, for example, is generally above (below) normal (see table 1 in Emery and Hamilton 1985).

By giving several examples of significant correlations between oceanic and fishery fluctuations, together with detailed information on interannual variability in the northeast Pacific, I hope this review will stimulate further research on fish–environment interactions in which specific hypotheses are tested by field, laboratory, and theoretical studies. (See also Leggett (1984) for further amplification on this point in connection with future studies on fish migrations in the Atlantic.)

Although the topic of this paper has been tropical Pacific ENSO episodes and the related PNA teleconnection, large-scale interannual oceanic and atmospheric fluctuations have also been documented in other parts of the globe (e.g. Hastenrath 1976, 1984; Chu 1983; Marques et al. 1983; Picaut et al. 1984; Tourre and Rasmusson 1984). Further, some of these fluctuations are related through the teleconnection patterns given in Table 2. A subset of these oscillations may produce the 15–20 yr cycle seen in the records of the St. Lawrence River discharge and northwest Atlantic SST (Sutcliffe 1973; Loucks and Sutcliffe 1978). Moreover, these investigators found the above fluctuations to be highly correlated with the variations in several Scotian Shelf and Gulf of Maine fish stocks. Curiously enough, during this century, the major ENSO events have occurred roughly at 15–20 yr intervals (e.g. in 1925–26, 1940–41, 1957–58, and 1982–83; see also Fig. 35 for evidence of the 15–20 yr cycle in the British Columbia SST records). However, the "peak" years are approximately 180° out of phase with the northwest Atlantic environmental fluctuations studied by Louks and Sutcliffe: the discharge and temperature records show peaks at around 1930, 1950, and 1970. It is possible that these Atlantic fluctuations are somehow dynamically coupled to the strong ENSO events that are observed in most of the Pacific?

Acknowledgments

It is a pleasure to thank Drs. C. Groot, K. Hamilton, T. R. Parsons, and T. P. Quinn for their critical comments on a first draft of this paper, numerous colleagues who provided prints for the figures, the referees for their suggestions, and Nancy Oikawa for her assistance in the technical preparation of the manuscript. This work was supported by the Natural Sciences and Engineering Research Council of Canada through strategic grant G-1485.

References

BAKUN, A., AND R. H. PARRISH. 1980. Environmental inputs to fishery population models for eastern boundary current regions, p. 67–104. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variations in the survival of larval pelagic fishes. Intergov. Ocean. Comm. Workshop Rep. 28.

BARBER, R. T., AND F. P. CHAVEZ. 1983. Biological consequences of El Niño. Science (Wash., DC) 222: 1203–1210.

BJERKNES, J. 1966. The possible response of the atmospheric Hadley circulation to equatorial anomalies of ocean temperature. Tellus 4: 820–829.

1969. Atmospheric teleconnections from the equatorial Pacific. Mon. Weather Rev. 77: 163–172.

1972. Atmospheric response to the 1964–65 Pacific equatorial warming. J. Phys. Oceanogr. 2: 212–217.

BLACKMON, M. L., Y.-H. LEE, AND J. M. WALLACE. 1984. Horizontal structure of 500 mb height fluctuations with long, intermediate and short time scales. J. Atmos. Sci. 41: 961–979.

BOYD, J. P. 1980a. The nonlinear equatorial Kelvin wave. J. Phys. Oceanogr. 10: 1–11.

1980b. Equatorial solitary waves — Part I: Rossby solitons. J. Phys. Oceanogr. 10: 1699–1717.

BRINK, K. H. 1982. A comparison of long coastal trapped wave theory with observations off Peru. J. Phys. Oceanogr. 12: 897–913.

BURGNER, R. L. 1980. Some features of ocean migrations and timing of Pacific salmon, p. 153–164. *In* W. J. McNeil and D. C. Hinsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

BUSALACCHI, A. J., AND J. J. O'BRIEN. 1981. Interannual variability of the equatorial Pacific in the 1960's. J. Geophys. Res. 86: 10901–10907.

BUSALACCHI, A. J., AND M. A. CANE. 1985. Hindcasts of sea level variations during the 1982–83 El Niño. J. Phys. Oceanogr. 15: 213–221.

CANE, M. A. 1983. Oceanographic events during El Niño. Science (Wash., DC) 222: 1189–1195.

1984. Modeling sea level during El Niño. J. Phys. Oceanogr. 14: 1864–1874.

CHELTON, D. B. 1984. Short-term climatic variability in the northeast Pacific Ocean, p. 87–99. *In* W. G. Pearcy [ed.] The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis, OR.

CHELTON, D. B., P. A. BERNAL, AND J. A. MCGOWAN. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40: 1095–1125.

CHELTON, D. B., AND R. E. DAVIS. 1982. Monthly mean sea-level variability along the west coast of North America. J. Phys. Oceanogr. 12: 757–784.

CHU, P.-S. 1983. Diagnostic studies of rainfall anomalies in northeast Brazil. Mon. Weather Rev. 111: 1655–1664.

COLIN, C., C. HENIN, P. HISARD, AND C. OUDOT. 1971. Le Courant de Cromwell dans le Pacifique central en Février. Cah. ORSTOM Oceanogr. 9: 167–186.

CUSHING, D. H. 1982. Climate and fisheries. Academic Press, New York, NY. 373 p.

DAVIS, R. E. 1976. Predictability of sea surface temperature and sea level pressure anomalies over the North Pacific Ocean. J. Phys. Oceanogr. 6: 249–266.

EGGERS, D. M., C. P. MEACHAM, AND D. C. HUTTERNEN. 1984. Population dynamics of Bristol Bay sockeye salmon, 1956–1983, p. 200–225. *In* W. G. Pearcy [ed.] The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis, OR.

EMERY, W. J., AND K. HAMILTON. 1985. Atmospheric forcing of interannual variability in the northeast Pacific Ocean, connections with El Niño. J. Geophys. Res. 90: 857–868.

EMERY, W. J., W. G. LEE, AND L. MAGAARD. 1984. Geographic and seasonal distribution of Brunt-Väisälä frequency and Rossby radii in the North Pacific and North Atlantic. J. Phys. Oceanogr. 14: 294–317.

EMERY, W. J., T. C. ROYER, AND R. W. REYNOLDS. 1985. The anomalous tracks of North Pacific drifting buoys 1981 to 1983. Deep-Sea Res. 32: 315–347.

ENFIELD, D. B. 1981. Thermally driven wind variability in the planetary boundary layer above Lima, Peru. J. Geophys. Res. 86: 2005–2016.

ENFIELD, D. B., AND J. S. ALLEN. 1980. On the structure and dynamics of monthly mean sea level anomalies along the Pacific coast of North and South America. J. Phys. Oceanogr. 10: 557–578.

ERIKSEN, C. C., M. B. BLUMENTHAL, S. P. HAYES, AND P. RIPA. 1983. Wind-generated equatorial Kelvin waves observed across the Pacific Ocean. J. Phys. Oceanogr. 13: 1622–1640.

FAVORITE, F. 1961. Surface temperatures and salinity off the Washington and British Columbia coasts, August 1958 and 1959. J. Fish. Res. Board Can. 18: 311–319.

FAVORITE, F., AND D. R. MCLAIN. 1973. Coherence in transpacific movements of positive and negative anomalies of sea surface temperature, 1953–1960. Nature (Lond.) 224: 139–143.

FIRING, E., R. LUKAS, J. SADLER, AND K. WYRTKI. 1983. Equatorial Undercurrent disappears during 1982–83 El Niño. Science (Wash., DC) 222: 1121–1123.

FRANCIS, R. C., AND K. M. BAILEY. 1983. Factors affecting recruitment of selected gadoids in the northeast Pacific and east Bering Sea, p. 35–60. *In* W. S. Wooster [ed.] From year to year. Washington Sea Grant, Seattle, WA.

FREELAND, H. J., AND L. F. GIOVANDO. 1984. The 1982–83 Pacific Ocean warm event off British Columbia. Trop. Ocean-Atmos. Newslett. 23: 18–19.

FULTON, J. 1983. Seasonal and annual variations of net zooplankton at Ocean Station 'P', 1956–1980. Can. Data Rep. Fish. Aquat. Sci. 374: 65 p.

FULTON, J. D., AND R. J. LEBRASSEUR. 1985. Interannual shifting of the subarctic boundary and some of the biotic effects on juvenile salmonids, p. 237–252. *In* W. S. Wooster and D. L. Fluharty [ed.] El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant, Seattle, WA.

GILL, A. E., AND E. M. RASMUSSON. 1983. The 1982–83 climate anomaly in the equatorial Pacific. Nature (Lond.) 306: 229–234.

GREATBATCH, R. J. 1985. Kelvin wave fronts, Rossby solitary waves and the nonlinear spin-up of the equatorial oceans. J. Geophys. Res. 90: 9097–9107.

GROOT, C., L. MARGOLIS, AND R. BAILEY. 1984. Does the route of the seaward migration of Fraser River sockeye salmon (*Oncorhynchus nerka*) smelts determine the route of return migration of the adults?, p. 283–292. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Press, New York, NY.

HALPERN, D., S. P. HAYES, A. LEETMAA, D. V. HANSEN, AND S. G. H. PHILANDER. 1983. Oceanographic observations of the 1982 warming of the eastern tropical Pacific. Science (Wash., DC) 221: 1173–1175.

HAMILTON, K. 1985. A study of the variability of the return migration route of Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Zool. 63: 1930–1943.

HAMILTON, K., AND L. A. MYSAK. 1986. Possible effects of the Sitka eddy on sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) migration off southeast Alaska. Can. J. Fish. Aquat. Sci. 43. (In press)

HANEY, R. L. 1980. A numerical case study of the development of large-scale thermal anomalies in the central North Pacific Ocean. J. Phys. Oceanogr. 10: 541–556.

HANEY, R. L., B. H. HOUTMAN, AND W. H. LITTLE. 1983. The relationship between wind and sea surface temperature anomalies in the midlatitude North Pacific Ocean. Atmosphere-Ocean 21: 168–186.

HARRISON, D. E., AND P. S. SCHOPF. 1984. Kelvin-wave-induced anomalous advection and the onset of surface warming in El Niño events. Mon. Weather Rev. 112: 923–933.

HASTENRATH, S. 1976. Variations in low-latitude circulation and extreme climate events in the tropical Americas. J. Atmos. Sci. 33: 202–215.

1984. Interannual variability and the annual cycle: mechanisms of circulation and climate in the tropical Atlantic sector. Mon. Weather Rev. 112: 1097–1107.

HIRST, A. C. 1985. Destabilization of equatorial ocean waves by atmosphere–ocean coupling. Trop. Ocean-Atmos. Newslett. 29: 16–18.

HOREL, J. D. 1982. On the annual cycle of the tropical Pacific atmosphere and ocean. Mon. Weather Rev. 110: 1863–1878.

HOREL, J. D., AND J. M. WALLACE. 1981. Planetary-scale atmospheric phenomena associated with the Southern Oscillation. Mon. Weather Rev. 109: 813–829.

HOSKINS, B. J., AND D. J. KAROLY. 1981. The steady linear response of a spherical atmosphere to thermal and orographic forcing. J. Atmos. Sci. 38: 1179–1196.

HOSKINS, B. J., A. J. SIMMONS, AND D. G. ANDREWS. 1977. Energy dispersion in a barotropic atmosphere. Q. J. R. Meterol. Soc. 103: 553–567.

HURLBURT, H. E., J. C. KINDLE, AND J. J. O'BRIEN. 1976. A numerical simulation of the onset of El Niño. J. Phys. Oceanogr. 6: 621–631.

HUSBY, D. M., AND C. S. NELSON. 1982. Turbulence and vertical stability in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 113–129.

INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION (IPSFC). 1984. Annual Report for 1983. 53 p.

KERR, R. A. 1983. Fading El Niño broadening scientists' view. Science

(Wash., DC) 221: 940–941.

KNOX, R. A., AND D. HALPERN. 1982. Long range Kelvin wave propagation of transport variations in Pacific Ocean equatorial currents. J. Mar. Res. 40 (Suppl.): 329–339.

KRAUS, E. B., AND H. P. HANSON. 1983. Air–sea interaction as a propagator of equatorial ocean surface temperature anomalies. J. Phys. Oceanogr. 13: 130–138.

LEBLOND, P. H., AND L. A. MYSAK. 1978. Waves in the ocean. Elsevier, New York, NY. 602 p.

LEBRASSEUR, R. J. 1965. Biomass atlas of net zooplankton in the Northeastern Pacific Ocean, 1956–1964. Fish. Res. Board Can. MS Rep. Ser. (Oceanogr. Limnol.) 201: 261 p.

LEETMAA, A. 1983. The role of local heating in producing temperature variations in the offshore waters of the eastern tropical Pacific. J. Phys. Oceanogr. 13: 467–473.

LEGGETT, W. C. 1984. Fish migrations in coastal and estuarine environments: a call for new approaches to the study of an old problem, p. 159–178. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Press, New York, NY.

LOUCKS, R. H., AND W. H. SUTCLIFFE JR. 1978. A simple fish-population model including environmental influence, for two western Atlantic shelf stocks. J. Fish. Res. Board Can. 35: 279–285.

LUDWIG, D., AND C. J. WALTERS. 1982. Optimal harvesting with imprecise paameter estimates. Ecol. Model. 14: 273–292.

LUTHER, D. S., D. E. HARRISON, AND R. A. KNOX. 1983. Zonal winds in the central equatorial Pacific and El Niño. Science (Wash., DC) 222: 327–330.

MAGAARD, L. 1983. On the potential energy of baroclinic Rossby waves in the North Pacific. J. Phys. Oceanogr. 13: 38–42.

MARQUES, V. S., V. B. RAO, AND L. C. MOLION. 1983. Interannual and seasonal variations in the structure and energetics of the atmosphere over northeast Brazil. Tellus 35: 136–148.

MCCLEAVE, J. D., G. P. ARNOLD, J. J. DODSON, AND W. H. NIEL [ED.] 1984. Mechanisms of migration in fishes. Plenum Press, New York, NY. 574 p.

MCCREARY, J. P. JR. 1976. Eastern tropical ocean response to changing wind systems: with application to El Niño. J. Phys. Oceanogr. 6: 632–645.

1983. A model of tropical ocean–atmosphere interaction. Mon. Weather Rev. 111: 370–387.

MCCREARY, J. P. JR., AND D. L. T. ANDERSON. 1984. A simple model of El Niño and the Southern Oscillation. Mon. Weather Rev. 112: 934–946.

MCLAIN, D. R. 1984. Coastal warming in the northeast Pacific, 1976–83, p. 61–86. *In* W. G. Pearcy [ed.] The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis, OR.

MCLAIN, D. R., AND D. H. THOMAS. 1983. Year-to-year fluctuations of the California Countercurrent and effects on marine organisms. Calif. Coop. Oceanic Fish. Invest. Rep. 24: 165–181.

MOORE, D. W., AND S. G. H. PHILANDER. 1977. Modeling of the tropical oceanic circulation, p. 319–361. *In* E. D. Goldberg, I. N. McCave, J. J. O'Brien, and J. H. Steele [ed.] The sea. John Wiley & Sons, New York, NY.

MYSAK, L. A. 1980. Recent advances in shelf wave dynamics. Rev. Geophys. Space Phys. 18: 211–241.

1985. On the interannual variability of eddies in the northeast Pacific Ocean, p. 97–106. *In* W. S. Wooster and D. L. Fluharty [ed.] El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant, Seattle, WA.

MYSAK, L. A., W. W. HSIEH, AND T. R. PARSONS. 1982. On the relationship between interannual baroclinic waves and fish population in the northeast Pacific. Biol. Oceanogr. 2: 63–103.

NAMAIS, J. 1976. Some statistical and synoptic characteristics associated with El Niño. J. Phys. Oceanogr. 6: 130–138.

NAMAIS, J., AND R. M. BORN. 1972. Empirical techniques applied to large-scale and long-period air–sea interactions, a preliminary report. SIO Ref. Ser. 72-1, Scripps Institution of Oceanography, University of California, San Diego, CA. 47 p.

PAN, Y. H., AND A. H. OORT. 1983. Global climate variations connected with sea surface temperature anomalies in the eastern equatorial Pacific Ocean for the 1958–73 period. Mon. Weather Rev. 111: 1244–1258.

PEARCY, W. G. 1983. Commentary: abiotic variations in regional environments, p. 30–34. *In* W. D. Wooster [ed.] From year to year. Washington Sea Grant, Seattle, WA.

PEARCY, W. G. [ed.] 1984. The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis, OR. 327 p.

PETERSON, W. T., AND R. L. SMITH. 1979. Upwelling indices and the Oregon Dungeness crab fishery catches, p. 132–133. *In* J. Knauss [ed.] Climate and fisheries. University of Rhode Island Press, Kingston, RI.

PHILANDER, S. G. H. 1981. The response of equatorial oceans to a relaxation of the trade winds. J. Phys. Oceanogr. 11: 176–189.

1983. Anomalous El Niño of 1982–83. Nature (Lond.) 305: 16.

PHILANDER, S. G. H., T. YAMAGATA, AND R. C. PACANOWSKI. 1984. Unstable air–sea interactions in the tropics. J. Atmos. Sci. 41: 604–613.

PICAUT, J., J. SERVAIN, A. J. BUSALACCHI, AND M. SEVA. 1984. Interannual variability versus seasonal variability in the tropical Atlantic. Geophys. Res. Lett. 11: 787–790.

QUINN, W. H., D. O. ZOPF, K. S. SHORT, AND R. T. W. K. YANG. 1978. Historical trends and statistics of the Southern Oscillation, El Niño, and Indonesian droughts. Fish. Bull. 76: 663–678.

RADOVICH, J. 1961. Relationships of some marine organisms of the North Pacific to water temperatures, particularly during 1957–59. Calif. Dep. Fish Game Mar. Res. Oper. Fish. Bull. 112: 62 p.

RASMUSSON, E. M., AND T. H. CARPENTER. 1982. Variations in tropical sea surface temperature and surface wind fields associated with the Southern Oscillation/El Niño. Mon. Weather. Rev. 110: 354–384.

RASMUSSON, E. M., AND J. M. WALLACE. 1983. Meteorological aspects of the El Niño/Southern Oscillation. Science (Wash, DC) 222: 1195–1202.

RENNICK, M. A., AND R. L. HANEY. 1985. Stability of some simple coupled models. Trop. Ocean-Atmos. Newslett. 29: 18–19.

REYNOLDS, R. W., AND E. M. RASMUSSON. 1983. The North Pacific sea surface temperature associated with El Niño events, p. 298–310. *In* Proceedings of the 7th Climate Diagnostic Workshop. U.S. Department of Commerce, NOAA, Washington, DC.

RODEN, G. I. 1958. Spectral analysis of sea-surface temperature and atmospheric pressure off Southern California. J. Mar. Res. 16: 90–95.

1966. Low-frequency sea level oscillations along the Pacific coast of North America. J. Geophys. Res. 71: 4755–4776.

ROGERS, D. E. 1980. Density-dependent growth of Bristol Bay sockeye salmon, p. 267–283. *In* W. J. McNeil and D. C. Hinsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

1984. Trends in abundance of northeastern Pacific stocks of salmon, p. 100–127. *In* W. G. Pearcy [ed.] The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis, OR.

ROYAL, L. A., AND J. P. TULLY. 1961. Relationship of variable oceanographic factors to migration and survival of Fraser River salmon. Calif. Coop. Oceanic Fish. Invest. Rep. 8: 65–68.

ROYCE, W. F., L. S. SMITH, AND A. C. HARTT. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. Fish. Bull. 66: 441–462.

SCHOPF, P. S., AND D. E. HARRISON. 1983. On equatorial waves and El Niño. I.: Influence of initial states on wave-induced currents and warming. J. Phys. Oceanogr. 13: 936–948.

SEMTNER, A. J., AND W. R. HOLLAND. 1980. Numerical simulation of equatorial ocean circulation. Part I.: A basic case for turbulent equilibrium. J. Phys. Oceanogr. 10: 667–693.

SHEPHERD, J. G., AND J. W. HORWOOD. 1979. The sensitivity of exploited populations to environmental "noise", and the implications for management. J. Cons. Int. Explor. Mer 38: 318–323.

SIMMONS, A. J., J. M. WALLACE, AND G. W. BRANSTATOR. 1983. Barotropic wave propagation, instability and atmospheric teleconnection patterns. J. Atmos. Sci. 40: 1363–1392.

SIMPSON, J. J. 1983. Large-scale thermal anomalies in the California Current during the 1982–83 El Niño. Geophys. Res. Lett. 10: 937–940.

SINCLAIR, M., M. J. TREMBLAY, AND P. BERNAL. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

SMITH, R. L. 1983. Peru coastal currents during El Niño: 1976 and 1982. Science (Wash., DC) 221: 1397–1399.

SOUTAR, A., AND J. D. ISAACS. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. 72: 257–273.

SUGINOHARA, N. 1981. Propagation of coastal-trapped waves at low latitudes in a stratified ocean with continental shelf slope. J. Phys. Oceanogr. 11: 1113–1122.

SUTCLIFFE, W. H. JR. 1973. Correlations between seasonal river discharge and local landings of American lobster (*Homasrus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 30: 856–859.

SWATERS, G. E., AND L. A. MYSAK. 1985. Topographically induced baroclinic eddies near a coastline, with application to the northeast Pacific. J. Phys. Oceanogr. 15: 1470–1485.

TABATA, S. 1981. Oceanic time-series measurements from Station P and along Line P in the northeast Pacific Ocean, p. 171–192. *In* D. J. Ellett [ed.] World Climate Program 21. World Meteorological Organization, Geneva, Switzerland.

1982. The anticyclonic, baroclinic eddy off Sitka, Alaska, in the northeast Pacific. J. Phys. Oceanogr. 12: 1260–1282.

1984a. Oceanographic conditions off the Pacific coast of Canada during the 1982–1983 El Niño, p. 92–99. *In* Proceedings of the 8th Climate Diagnostic Workshop. U.S. Department of Commerce, NOAA, Washington, DC.

1984b. Anomalously warm water off the Pacific coast of Canada during the 1982–83 El Niño. Trop. Ocean-Atmos. Newslett. 24: 7–9.

1984c. Oceanographic factors influencing the distribution, migration, and survival of salmonids in the northeast Pacific Ocean — a review, p. 128–160. *In* W. G. Pearcy [ed.] The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University Press, Corvallis, OR.

THOMSON, R. E., H. J. FREELAND, AND L. F. GIOVANDO. 1984. Long-term sea surface temperature variations along the British Columbia coast. Trop. Ocean-Atmos. Newslett. 26: 9–11.

THOMSON, R. E., AND S. TABATA. 1981. Sea levels in the eastern Pacific Ocean, p. 137–154. *In* D. J. Ellett [ed.] World Climate Program 21. World Meteorological Organization, Geneva, Switzerland.

TOURRE, Y., AND E. RASMUSSON. 1984. The tropical Atlantic region during the 1982–83 equatorial Pacific warm event. Trop. Ocean-Atmos. Newslett. 25: 1–2.

TRENBERTH, K. E. 1976. Spatial and temporal variations of the Southern Oscillation. Q. J. R. Meteorol. Soc. 102: 639–653.

TULLY, J. P., A. J. DODIMEAD, AND S. TABATA. 1960. An anomalous increase of temperature in the ocean off the Pacific coast of Canada through 1957 and 1958. J. Fish. Res. Board Can. 17: 61–80.

TYLER, A. V. 1983. Commentary: The study of environmental effects on interannual variability in flatfish, p. 81–85. *In* W. S. Wooster [ed.] From year to year. Washington Sea Grant, Seattle, WA.

U.S. CLIMATE RESEARCH COMMITTEE. 1983. El Niño and the Southern Oscillation, a scientific plan. National Academy Press, Washington, DC. 72 p.

VAN LOON, H., AND R. A. MADDEN. 1981. The Southern Oscillation. Part I.: Global associations with pressure and temperature in northern winter. Mon. Weather Rev. 109: 1150–1162.

WAGNER, A. J. 1984. Possible mid-latitude atmospheric generation of anomalously warm surface waters in the Gulf of Alaska from autumn 1982 to spring 1983. Trop. Ocean-Atmos. Newslett. 26: 15–16.

WALLACE, J. M., AND D. S. GUTZLER. 1981. Teleconnections in the geopotential height field during the northern hemisphere winter. Mon. Weather Rev. 109: 784–812.

WEARE, B. C. 1983. Interannual variation in net heating at the surface of the tropical Pacific Ocean. J. Phys. Oceanogr. 13: 873–885.

WEARE, B. C., A. R. NAVATO, AND R. E. NEWELL. 1976. Empirical orthogonal analysis of Pacific sea surface temperatures. J. Phys. Oceanogr. 6: 671–678.

WEBSTER, P. J. 1981. Mechanisms determining the atmospheric response to sea surface temperature anomalies. J. Atmos. Sci. 38: 554–571.

WEBSTER, P. J., AND J. R. HOLTON. 1982. Cross equatorial response to middle-latitude forcing in a zonally varying basic state. J. Atmos. Sci. 39: 722–733.

WHITE, W. B., AND S. PAZAN. 1985. A prediction filter for forecasting the 1982–83 ENSO event. *In* Program of the IAMAP/IAPSO Joint Assembly, August 5–16, 1985, Honolulu, HI. p. 30 (Abstr.)

WHITE, W. B., AND J. F. T. SAUR. 1983. Sources of interannual baroclinic waves in the eastern subtropical North Pacific. J. Phys. Oceanogr. 13: 531–544.

WICKETT, W. P. 1975. Recent changes in the marine climate affecting herring, p. 39–43. *In* D. N. Outram [ed.] Proceedings of the Second Annual Pacific Coast Herring Workshop. Fish. Res. Board Can. MS Rep. 1342: 85 p.

1977. Relationship of coastal oceanographic factors to the migration of Fraser River sockeye salmon (*Oncorhynchus nerka*, W). Int. Comm. Explor. Sea. CM 1977/M.26: 18 p.

WOOSTER, W. S. [ED.] 1983a. From year to year. Washington Sea Grant, Seattle, WA. 208 p.

1983b. On the determinants of stock abundance, p. 1–10. *In* W. S. Wooster [ed.] From year to year. Washington Sea Grant, Seattle, WA.

WRIGHT, P. B. 1985. The Southern Oscillation: an ocean–atmosphere feedback system? Bull. Am. Meteorol. Soc. 66: 398–412.

WYRTKI, K. 1975. El Niño — the dynamic response of the equatorial Pacific Ocean to atmospheric forcing. J. Phys. Oceanogr. 5: 572–584.

1982. The Southern Oscillation, ocean–atmosphere interaction and El Niño. Mar. Tech. Soc. J. 16: 3–10.

YAMANAKA, H. 1984. The relationship between El Niño episodes and fish migrations and yields in the western Pacific. Trop. Ocean-Atmos. Newslett. 25: 2–4.

YAO, T., H. J. FREELAND, AND L. A. MYSAK. 1984. A comparison of low-frequency current observations off British Columbia with coastal-trapped wave theory. J. Phys. Oceanogr. 14: 22–34.

NOTE

Possible Effects of the Sitka Eddy on Sockeye (*Oncorhynchus nerka*) and Pink Salmon (*Oncorhynchus gorbuscha*) Migration off Southeast Alaska

Kevin Hamilton[1] and Lawrence A. Mysak[2]

Department of Oceanography, University of British Columbia, Vancouver, B.C. V6T 1W5

Hamilton, K., and L. A. Mysak. 1986. Possible effects of the Sitka eddy on sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) migration off southeast Alaska. Can. J. Fish. Aquat. Sci. 43: 498–504.

The interannual variability of sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) catches during 1952–62 from southeast Alaska and northern British Columbia is examined in relation to the appearance and disappearance of the Sitka eddy in the offshore oceanic circulation. In years when this large (~300 km in diameter) and intense (surface currents ~0.5 m/s) vortex is present, the spawning migration routes of salmon returning to the Nass and Skeena rivers tend to be deflected southward. An analysis of salmon tagging data collected during 1957 (when the eddy was absent) and 1958 (when the eddy was present) supports this conclusion. The southward deflection during 1958 is a particularly interesting result in light of many other observations which show that several fish species were displaced northward during the 1958 warming of the northeast Pacific Ocean.

On étudie les variations d'une année à l'autre des prises de saumons rouges (*Oncorhynchus nerka*) et de saumons roses (*Oncorhynchus gorbuscha*) effectuées entre 1952 et 1962 au sud-est de l'Alaska et au nord de la Colombie-Britannique, par rapport à l'apparition et à la disparition du remous Sitka dans la circulation océanique au large. Les années où ce tourbillon important (diamètre d'environ 300 km) et intense (courants de surface d'environ 0,5 m/s) est présent, les routes de migration des saumons qui reviennent frayer dans les rivières Nass et Skeena ont tendance à être déviées vers le sud. Une analyse des données d'étiquetage de saumons recueillies en 1957 (lorsque le remous était absent) et en 1958 (lorsque le remous était présent) appuie cette conclusion. La déviation vers le sud en 1958 est un résultat particulièrement intéressant compte tenu d'un grand nombre d'autres observations qui montrent que plusieurs espèces de poisson se sont déplacées vers le nord, lors du réchauffement, en 1958, du nord-est de l'océan Pacifique.

Received February 4, 1985
Accepted October 16, 1985
(J8104)

Reçu le 4 février 1985
Accepté le 16 octobre 1985

The return migration of adult salmon (*Oncorhynchus*) from the open ocean to the various spawning rivers in northern British Columbia and southeast Alaska has been a subject of scientific investigation for over half a century (e.g. Rich 1926; Noerenberg 1959; Alaska Department of Fish and Game 1984). A knowledge of the details of the migration routes in this area (and of the year-to-year variability in these routes) is important both for optimal management of the salmon stocks and for the formulation of policies allowing a rational division of the catch between the Canadian and American fisheries. At present there is an international, multi-million dollar project underway to assess the proportions of American- and Canadian-bred salmon in the commercial catches of the two countries (Alaska Department of Fish and Game 1984). Our purpose here is to relate the return migration route of salmon in this region to a spectacular feature of the offshore oceanic circulation, the so-called Sitka eddy.

Sitka Eddy

The Sitka eddy is a large (~300 km in diameter) clockwise-rotating vortex that is observed in some years off the southeast Alaska coast, centered near 57°N, 138°W. Since the surface currents in this eddy can exceed 0.5 m/s (1 knot), it was suggested by Mysak (1986) that the migration routes of returning sockeye (*O. nerka*), for example, could be significantly altered by the presence of the eddy (note that the swimming speed of

[1]Present address: Department of Meteorology, McGill University, Montreal, P.Q. H3A 2K6.

[2]Also Department of Mathematics and Institute of Applied Mathematics, University of British Columbia.

a mature sockeye is typically 0.5 m/s).

Tabata (1976, 1982) analyzed hydrographic data (i.e. temperature and salinity throughout the water column) taken during several survey cruises of the northeast Pacific Ocean in the 1950s and 1960s. Figure 1 shows the geopotential anomalies at the surface computed by Tabata for each year in which there are data during either the spring or summer. The geopotential anomaly can be interpreted as the horizontal distribution of pressure that drives the surface currents. The mesoscale oceanic circulation here is known to be very nearly geostrophic: thus, the surface currents should be directed almost parallel to the contours of Fig. 1, and the magnitude of the current should be related to the gradient of the geopotential anomaly (i.e. closely spaced contours reflect intense currents).

The region of closely spaced closed contours off southeast Alaska, which can be clearly seen in the 1958, 1960, and 1961 data in Fig. 1, is the surface geopotential manifestation of the Sitka eddy. Despite incomplete data coverage, it seems likely that the eddy was also present in 1954. On the other hand, there is sufficient data to show unequivocably that the eddy was not present in 1957, 1959, and 1962. Thus, on the basis of this small sample, one might conclude that the eddy is present in the spring and summer of about one out of every two years. Unfortunately, hydrographic observations with high spatial resolution were not continued in this region in later years, and so Fig. 1 apparently summarizes all the useful data of this sort. When the eddy does appear in the observations, it generally has a diameter of about 300 km and is centered 200–300 km west of Sitka, which is located on Baranof Island (see Fig. 2). The flow in the eddy is always anticyclonic (i.e. clockwise looking from above), but the precise form of the flow field varies from year to year (and is also observed to change somewhat during the course of a single year, see Tabata 1982).

Mechanisms for the generation and evolution of the Sitka eddy have been investigated by Willmott and Mysak (1980) and Swaters and Mysak (1985). There are several large bottom topographic features off the southeast Alaska coast and it is probable that the eddy is generated by the interaction of the ambient northward coastal current with these topographic irregularities (this could explain the approximately constant location of the eddy when it occurs). However, it appears that the upstream current must lie in a certain critical range of speeds in order for the eddy to be trapped over the topography (Swaters and Mysak 1985). If this criterion is not satisfied, no eddy can be generated through this mechanism (this may explain its absence in some years). Once the eddy has been generated, it is likely that long time scale dynamics associated with interannual Rossby waves become important (Willmott and Mysak 1980); this may produce the slow westward drift of the eddy which has been observed by Tabata (1982).

The horizontal currents associated with the Sitka eddy extend down to depths of at least 1000 m (Tabata 1982), but it is the surface and near-surface currents that are likely to be of significance for salmon migration. The current speeds in each panel of Fig. 1 can be determined using the geostrophic current scale shown in the lower left-hand side in each case (using the spacing in the scale for a latitude of about 55°N). For example, the very regularly spaced contours in the southeastern portion of the eddy in July–September 1960 reflect surface currents of 0.1–0.2 m/s. In many cases, however, the geopotential gradients in the eddy are much larger, and current speeds in the range 0.5–1.0 m/s may be found. These current magnitudes can be compared with the typical 0.5 m/s swimming speed of an adult sockeye salmon in its oceanic migration (C. Groot and T. Quinn, Pacific Biological Station, Nanaimo, B.C., per. comm.). Thus, a salmon traversing the eddy (and spending a few days within it) could be significantly deflected by the surface currents.

Salmon Migration Routes

The gross features of the migrations of Pacific sockeye and pink (*O. gorbuscha*) salmon have been documented through extensive tagging studies (e.g. Royce et al. 1968; French et al. 1976). During their final winter at sea, the salmon are known to commence their homeward spawning migration. In the process, each population converges towards the mouth of its particular river system. A majority of salmon returning to the west coast of North America initially head slightly north of their natal rivers, and the final stretch of the oceanic migration is probably from the northwest (e.g. fig. 7 of Royce et al. 1968).

Given the complicated coastline of the Alaskan Panhandle (Fig. 2), there are many possible routes for their final migration paths. For example, fish returning to the Nass and Skeena rivers of northern British Columbia could come from the ocean directly through Dixon Entrance, they could make landfall on the outer coast of Prince of Wales Island and then move southwards down that coast, or they could even penetrate to the inner Alaskan coast somewhere north of Prince of Wales Island and then head south through the inner passages. Recent tagging studies (Alaska Department of Fish and Game 1984) have shown that the vast majority of Nass/Skeena sockeye actually come in either directly through Dixon Entrance or down the outer coast of Prince of Wales Island. These two migration routes are shown schematically by the heavy tracks in Fig. 2. The Alaskan tagging study did not specifically consider pink salmon, but it is known that many Nass and Skeena pinks are found in the commercial catch made along the west coast of Prince of Wales Island (e.g. Noerenberg 1959). Thus, it is likely that pink salmon also possess the potential for a variability in the final return migration route similar to that documented for the sockeye.

Interannual changes in the proportions of Nass/Skeena salmon returning via the two routes shown as heavy tracks in Fig. 2 could have some significant practical consequences. In particular, those fish returning via the coast of Prince of Wales Island can be intercepted by the American commercial seine fishery that operates on this coast (and around the small islands off the coast), while those returning directly from the open ocean into Dixon Entrance would not be available to the Americans. It has been conjectured (Mysak 1985) that such route changes could be produced by the unusually strong currents associated with the Sitka eddy.

If the final leg of the migration of salmon heading for the coast is made in a generally southeastward direction, then a significant fraction of the fish that reach either Prince of Wales Island or Dixon Entrance have probably passed through the Sitka eddy. If a fish enters the eddy unwittingly on the western side and is simply advected passively by the clockwise current, then it could be deflected to the northeast, as illustrated by track "a" in Fig. 2. On the other hand, fish encountering only the southern edge of the eddy could be passively advected westward.

Another set of possibilities would arise if the fish could sense the presence of the eddy. In particular, the migratory behaviour of the salmon in this region may have become adapted to

TABLE 1. Fraction returned from American and Canadian waters of salmon tagged west of Prince of Wales Island in 1957 and 1958 and ratio of Canadian to American returns (adapted from Noerenberg 1959). There were 11 478 pink and 499 sockeye tagged in 1957 and 4925 pink and 1483 sockeye tagged in 1958.

Year	Species	American	Canadian	Ratio
1957	Pink	0.283	0.158	0.558
1958	Pink	0.346	0.033	0.095
1957	Sockeye	0.186	0.188	1.011
1958	Sockeye	0.261	0.153	0.586

somehow account for the strong currents associated with the Sitka eddy. The occurrence of the eddy could possibly be sensed by the fish through the electric field associated with ocean currents (Royce et al. 1968), through a direct perception of current shears (Royce et al. 1968), or by detection of anomalies in biological productivity known to occur at the edge of oceanic eddies. Of interest with respect to the possible effects of ocean currents on salmon migratory behaviour are some very recent observations concerning the Fraser River sockeye spawning run in nearshore waters (T. Quinn and B. Terhart, University of British Columbia, Vancouver, B.C., pers. comm.). In particular, Quinn and Terhart have found a preference for the sockeye to swim into the current. If one imagines that Nass/Skeena salmon encountering the Sitka eddy in the open ocean have a similar preference, then fish entering the western portion of the eddy might tend to deflect southward (as illustrated by track "b" in Fig. 2). The tagging and commercial catch data to be discussed below suggest that the eddy actually causes a net southward and/or westward displacement of the migration routes of Nass/Skeena sockeye and pink salmon.

The migration routes of the homeward-bound salmon could, in principle, also be affected by the ocean currents they encounter throughout their entire journey. However, midoceanic current speeds are generally quite small (a few centimetres per second) and, assuming the salmon possess some kind of celestial or magnetic navigation system (e.g. Quinn 1984), they would have ample time to compensate for the effects of such currents by adjusting their swimming speed and orientation. Thus, the variability in offshore currents may have less influence in determining where the fish actually make landfall on the coast than the very strong currents (i.e. comparable with the fish swimming speed) that the salmon may encounter in the region of the Sitka eddy during the final brief stretch of their migration.

Tagging Experiments in 1957 and 1958

In 1957 and 1958, researchers at the University of Washington carried out a project involving the tagging of several thousand pink and sockeye salmon initially caught off the west coast of Prince of Wales Island. In retrospect, the choice of these two years for this study makes the results of particular interest, since it is now known that 1958 was characterized by extremely anomalous oceanographic conditions in the northeast Pacific. In particular, there was an intense warming trend throughout the period from the summer of 1957 through the summer of 1958; this was presumably associated with the very strong El Niño event of 1957–58. By the spring and summer of 1958, the sea surface temperature along and off the coasts of British Columbia and southeast Alaska was at least 1.5°

TABLE 2. Comparison of total annual catches of pink and sockeye salmon in Alaskan West Prince of Wales area (WPoW), which extends along almost the whole west coast of this island, and in British Columbia areas 3 and 4 (i.e. the Nass and Skeena catches), and Sitka eddy occurrence during the spring or summer of each year.

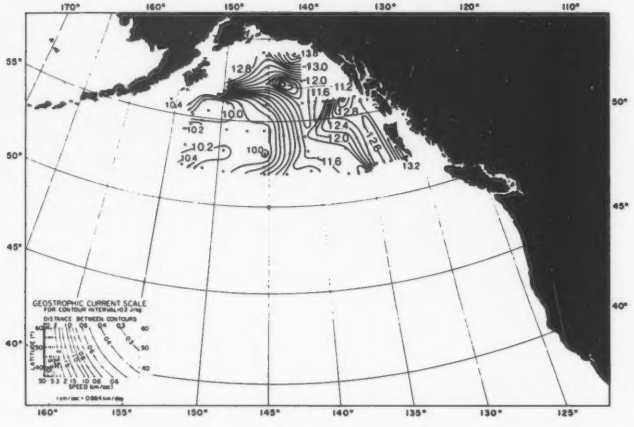
	Catch (thousands of fish)			
Year	WPoW	Areas 3 and 4	Catch ratio, Alaska/B.C.	Eddy present
		Pink salmon		
1952	1685.4	1741.5	0.968	Unknown
1953	1402.3	671.5	2.088	Unknown
1954	719.5	1302.2	0.552	Probably
1955	1661.4	1790.5	0.927	Unknown
1956	3177.1	1421.6	2.235	Unknown
1957	3274.8	3042.6	1.076	No
1958	1392.1	1583.0	0.879	Yes
1959	947.5	805.8	1.176	No
1960	577.4	254.4	2.269	Yes
1961	1533.9	1176.2	1.304	Yes
1962	1744.5	874.0	1.995	No
		Sockeye salmon		
1952	152.6	1599.0	0.095	Unknown
1953	211.2	857.6	0.246	Unknown
1954	192.1	673.5	0.285	Probbaly
1955	82.4	314.9	0.261	Unknown
1956	91.3	403.9	0.223	Unknown
1957	264.3	425.5	0.624	No
1958	99.5	1000.8	0.099	Yes
1959	225.4	422.9	0.533	No
1960	139.7	319.1	0.438	Yes
1961	67.6	1176.2	0.057	Yes
1962	141.1	703.3	0.201	No

warmer than normal (Tully et al. 1960; Namias 1979). Coincident with the warming, there appeared to be northward shifts of various features of the biology of the northeast Pacific as well. Thus, for example, the contour of the surface zooplankton biomass distribution in the northeast Pacific coastal region is known to have been further north in the winter of 1958 than in 1957 (Fulton and LeBrasseur 1985). It is also known that several fish species were observed at unusually high latitudes in 1958 (Radovich 1961). Even the British Columbia catch of whales was extremely anomalous in 1958 (Tully et al. 1960).

Of particular interest with regard to conditions in 1958 are the data recorded concerning the Fraser River sockeye spawning run. Tully et al. (1960) and Royal and Tully (1961) presented evidence suggesting that the Fraser sockeye made landfall on the outer coast of British Columbia further north than usual. Perhaps as a consequence of this, an anomalously large fraction of the Fraser sockeye were observed to make their homeward migration around the northern end of Vancouver Island through Johnstone Strait, thus eschewing the more conventional route through Juan de Fuca Strait. This general northward displacement of the sockeye migration routes might have been a direct response to the northward shift of the usual oceanic temperature structure or, as suggested by Mysak (1986), it may have been in response to changes in the food supply available to the fish.

If the migration routes of the Nass/Skeena salmon followed

August - September 1954



June - August 1958

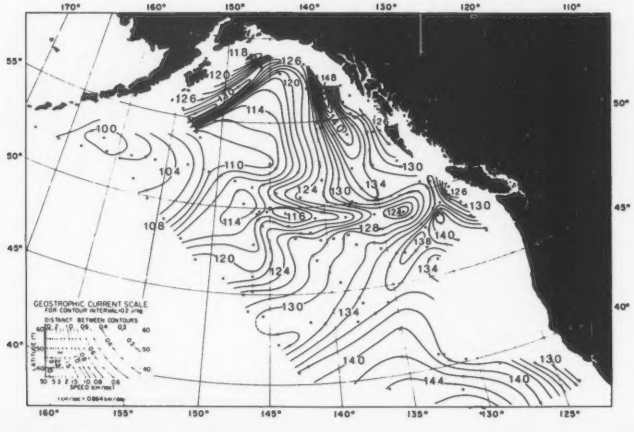
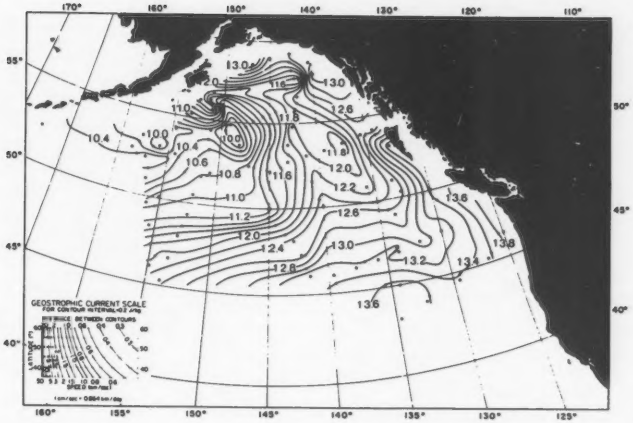
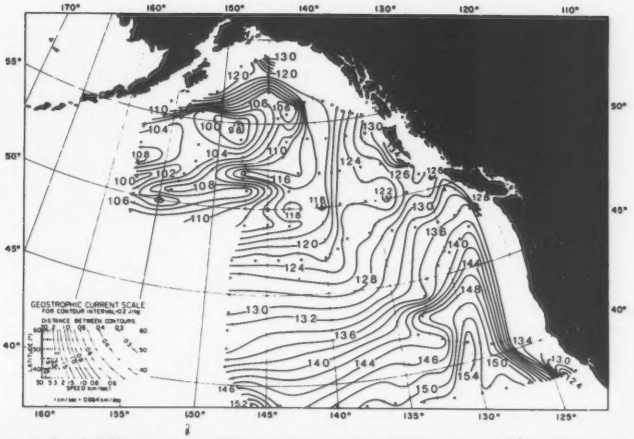


FIG. 1. Geopotential anomaly of the surface relative to a pressure of 1000 db in the sprin
velocity scale in each panel shows how the contour spacing is related to the magnitude of

July - August 1957

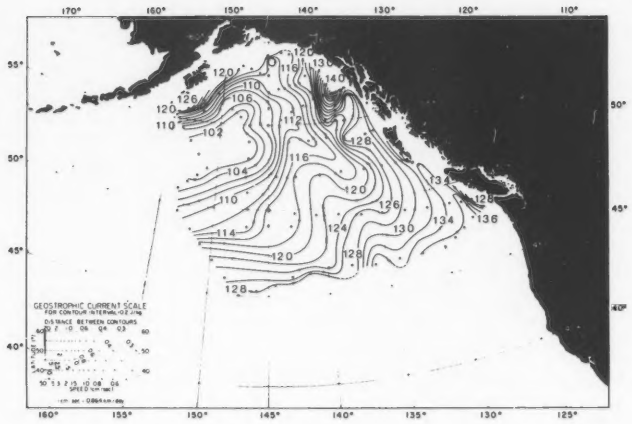


August - September 1959



he spring or summer periods of different years. The contours are labelled in units of J/kg. The geostrophic
itude of the surface geostrophic currents. (From Tabata 1982.)

July - September 1960



May - July 19

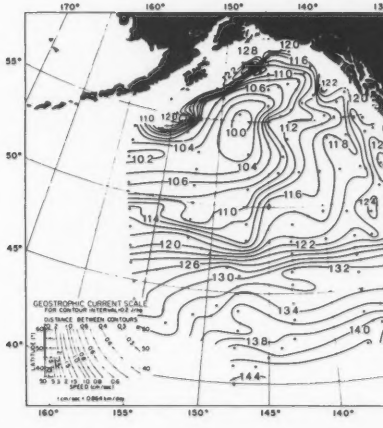
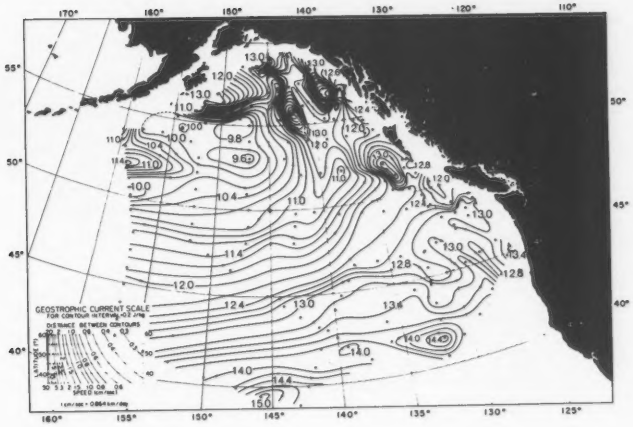
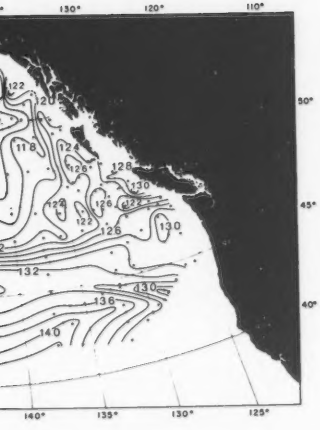


FIG. 1. (*Concluded*

May - July 1961



ly 1962



(*Concluded*)

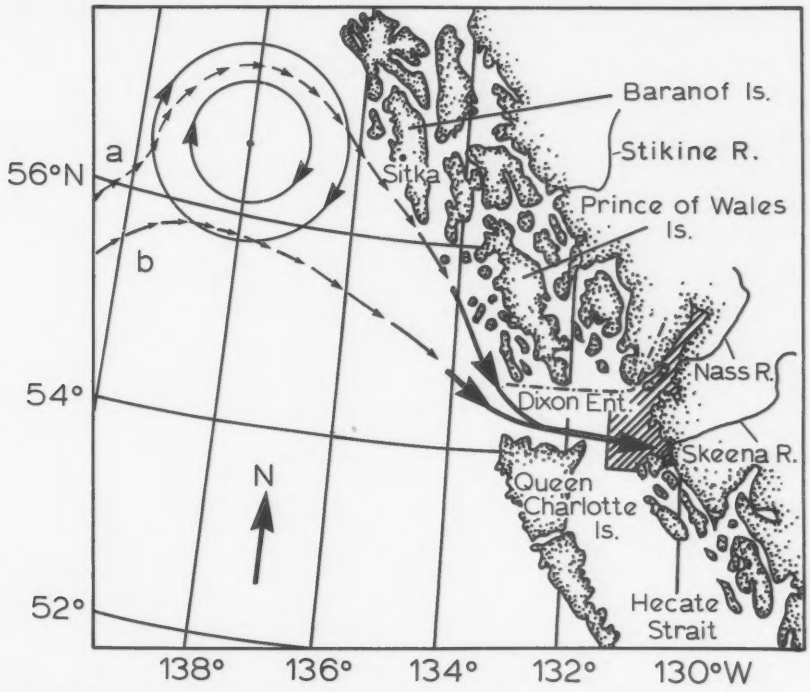


FIG. 2. Southeast Alaska – northern British Columbia coastal region. The concentric circles off Baranoff Island are a schematic representation of the currents associated with the Sitka eddy. The heavy tracks leading to the mouth of the Skeena River represent the range of migration routes taken by most sockeye according to fig. 27 of Alaska Department of Fish and Game (1984). The lighter arrows show how the migration path of a Nass or Skeena salmon might pass through the Sitka eddy. The shaded region represents British Columbia statistical areas 3 and 4. The dashed–dotted line is the international boundary.

the general pattern of the Fraser sockeye migration and of other aspects of the biology of the northeast Pacific, then it would be reasonable to expect a northward displacement of the migration routes of Nass/Skeena fish and thus that an anomalously large fraction of these fish would have tried to return down the coast of Prince of Wales Island in the summer of 1958. In actual fact, the results of the tagging studies of 1957 and 1958 suggest that just the opposite occurred. These results are summarized in Table 1. The ratio of the fractions of the tagged fish later found in Canadian waters to those returned from American waters gives a rough indication of the proportions of Canadian (mostly Nass/Skeena) and American (from the Stikine and other rivers) fish among those available to the fishery operating along the west coast of Prince of Wales Island. This ratio drops very sharply for both the pink and sockeye salmon from 1957 to 1958. This occurred despite the fact that 1958 was a particularly good year for Nass/Skeena sockeye (see Table 2). The most reasonable explanation for the drop in the ratio is that in 1958 more Nass/Skeena fish migrated directly from the open ocean through Dixon Entrance without making landfall on Prince of Wales Island.

The very peculiar results of the 1957–58 tagging studies might be explained in terms of the effect of the Sitka eddy on the migration of Nass/Skeena salmon. Inspection of Fig. 1 shows that the Sitka eddy was absent in the summer of 1957 but that it was present in something like its usual form in the summer of 1958. If the net effect of the eddy is to cause a diversion of Nass/Skeena fish to the south or southwest of the paths that they would take in the absence of the eddy, then in 1958 more Canadian salmon would have made their migration directly through Dixon Entrance (as in track "b" in Fig. 2) and fewer would appear in the American seine catch off of Prince of Wales Island.

Effects of the Sitka Eddy Revealed in Annual Catch Statistics

Since the early 1950s, Canadian and American government agencies have been collecting detailed commercial fish catch statistics in various regions. The statistics since 1952 have been summarized in yearbooks published by the International North Pacific Fisheries Commission. Given the strength and size of the Sitka eddy, it is reasonable to suppose that its presence or absence each year contributes in some manner to the interannual variability of these catch statistics. Table 2 summarizes some of the more relevant statistics for each year from 1952 through to 1962. In particular, Table 2 gives the pink and sockeye salmon catches along the west coast of Prince of Wales Island and in British Columbia statistical areas 3 and 4 (this latter represents the great bulk of the Canadian Nass and Skeena catches). Also listed is the ratio of these two values. Raw catch statistics of this kind will obviously be affected by other factors in addition to environmental influences, such as

the sizes of the spawning runs, fishing effort, etc. In particular, there are strong 2-yr cycles in the abundance of the pink salmon populations in the various river systems of the region. Despite all the possible sources of variability, however, there is still a trend evident in Table 2 for reduced American to Canadian catch ratios in years when the eddy is present. With the exception of the pink salmon statistics for 1960, the ratio always dropped whenever the eddy appeared after a year of absence, while the ratio always rose when the eddy disappeared.

The results in Table 2 are consistent with our view that the eddy tends to deflect a large portion of Nass/Skeena fish away from the American fishery. We suggest that this conclusion could be of some practical importance for the commercial fisheries operating in this region.

We recommend that future studies of salmon migration in the southeast Alaska region include some monitoring of the presence of this circulation feature. The ideal approach would be to conduct high-density hydrographic surveys around the time of the spawning run to uncover the detailed geostrophic current structure in each year. Since the eddy also appears as a warm sea surface temperature anomaly (at least in some years, see Tabata 1982), it may also be possible to obtain some indication of the presence or absence of the eddy through infrared satellite observations of the sea surface and/or through ship-of-opportunity or naval observations of the temperature patterns. A. Thomas (University of British Columbia, Vancouver, B.C., pers. comm.; see also fig. 6 in Mysak 1985) was recently able to identify the presence of the eddy during March 1983 in a single infrared image of the sea surface obtained with the University of British Columbia's satellite oceanographic laboratory.

Acknowledgments

We thank C. R. Forrester, S. Hoffman, P. A. Larkin, and J. Roos for helpful discussions and for providing data and D. J. Blackbourn for reading a first draft of this paper. We are also grateful to S. Tabata for supplying prints of the present Fig. 1. The work was supported by NSERC strategic grant G-1485.

References

ALASKA DEPARTMENT OF FISH AND GAME. 1984. Salmon research conducted in Southeast Alaska by the Alaska Department of Fish and Game in conjunction with National Marine Fisheries Service Auke Bay Laboratory for joint U.S.–Canada interception studies. 208 p.

FRENCH, R., H. BILTON, M. OSAKA, AND A. HARTT. 1976. Distribution and origin of sockeye salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 34: 113 p.

FULTON, J. D., AND R. J. LEBRASSEUR. 1985. Interannual shifting of the subarctic boundary and some of the biotic effects on juvenile salmonids, p. 237–252. *In* W. S. Wooster and D. L. Fluharty [ed.] El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant, Seattle, WA.

MYSAK, L. A. 1985. On the interannual variability of eddies in the Northeast Pacific Ocean, p. 97–106. *In* W. S. Wooster and D. L. Fluharty [ed.] El Niño North: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant, Seattle, WA.

1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43: 464–497.

NAMIAS, J. 1979. Northern hemisphere seasonal 700 mb height anomaly charts, 1947–1978, and associated North Pacific sea surface temperature anomalies. Calif. Coop. Oceanic Fish. Invest. Atlas No. 27: 275 p.

NOERENBERG, W. H. 1959. Salmon migrations in Southeast Alaska. U.S. Fish Wildl. Circ. 59: 8–12.

QUINN, T. P. 1984. An experimental approach to fish compass and map orientation, p. 113–123. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. M. Neill [ed.] Mechanisms of migration in fishes. Plenum Press, New York, NY.

RADOVICH, J. 1961. Relationships of some marine organisms of the North Pacific to water temperature, particularly during 1957–59. Calif. Dep. Fish Game Mar. Res. Oper. Fish. Bull. 112: 62 p.

RICH, W. S. 1926. Salmon tagging experiments in Alaska, 1924 and 1925. Fish. Bull. 42: 109–146.

ROYAL, L. A., AND J. P. TULLY. 1961. Relationship of variable oceanographic factors to migration and survival of Fraser River salmon. Calif. Coop. Fish. Invest. 8: 65–68.

ROYCE, W. F., L. S. SMITH, AND A. C. HARTT. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. Fish. Bull. 66: 441–462.

SWATERS, G. E., AND L. A. MYSAK. 1985. Topographically induced baroclinic eddies near a coastline, with application to the Northeast Pacific. J. Phys. Oceanogr. 15: 1470–1485.

TABATA, S. 1976. Evidence of a westward-flowing "Subarctic Countercurrent" in the North Pacific Ocean. J. Fish. Res. Board Can. 33: 2168–2196.

1982. The anticyclonic baroclinic eddy off Sitka, Alaska in the Northeast Pacific. J. Phys. Oceanogr. 12: 1260–1282.

TULLY, J. P., A. J. DODIMEAD, AND S. TABATA. 1960. An anomalous increase in temperature in the ocean off the Pacific coast of Canada through 1957 and 1958. J. Fish. Res. Board Can. 17: 61–80.

WILLMOTT, A. J., AND L. A. MYSAK. 1980. Atmospherically forced eddies in the Northeast Pacific. J. Phys. Oceanogr. 10: 1769–1791.

BOOK REVIEWS / COMPTES RENDUS

The restoration of rivers and streams: theories and experience. *Edited by James A. Gore. Butterworth Publishers, Stoneham, MA 02180. An Ann Arbor Science Book. 1985. xii + 280 p. $39.95 (U.S.).*

The editor, in his introduction, explains that his own involvement in a restoration project, on a western river that had been damaged by strip-mining, sparked his interest in the whole matter of restoration of watercourses after their degradation by man. He states that although there are several publications dealing with the subject, they tend to be specialized and inaccessible in government publications, and that he felt that a book was needed to bring theories, experiences, and techniques together in a volume that would be generally available.

To a great extent he has succeeded in his aim, although, as seems inevitable in any multi-authored work, the various chapters are uneven in their approach, and they cannot be described as integrated. There is, however, a general index, which allows the reader to have at least the feeling that this is a book rather than a collection of chapters.

The early chapters really carry the main thrust of the message. The first, by Herricks and Osborne, takes a quite philosophical approach to the impacts of land use upon rivers and streams, and points out that legal standards are, at best, not very satisfactory, and that they deal better with the problems of effluent discharges than they do with nonpoint sources of pollution. There follows a very interesting and informative chapter by Hasfurther on the factors that need to be considered in restoring an altered channel to a condition that is likely to be stable. He does this only in the context of a meandering channel, but his points apply in general to all efforts to constrain running water systems, and they are very suitable educational material for readers who are unlikely to be geomorphologists.

Anderson and Ohmart then deal with riparian vegetation along the Colorado River and their attempts to restore damaged areas as habitats for birds and mammals. This is, of itself, an interesting project, but it is a little off the main theme of the book because it seems to be as much concerned with battling with the introduced *Tamarix chinensis*, which is a local takeover weed, as with the problem of restoration of devastated areas.

There follow two chapters dealing with the practical aspects of restoration of invertebrate and fish habitats. Gore does this with special reference to the Tongue River in Wyoming, showing how fairly simple construction work increased the availability of habitats for invertebrates; but he also discusses invertebrate dispersal in a general way, and the timing of recovery in particular. I found that his demonstration that the predatory species were the last to stabilize their populations was particularly instructive, and I liked his suggestion that maybe they are the organisms that should be used to indicate recovery, rather than the various diversity indices that have been played with by so many environmental scientists. Wesche's chapter is also specialized in that it considers only Salmonidae in a western context. It does so, however, in a very practical way, giving details of techniques for creating suitable microhabitats by the construction of log-dams, artificial boulders, shelter along banks, etc. I believe that this account will be a valuable "how-to" document for many people involved in the management of inland fisheries, and that it brings together much of the expertise that is hidden away in official publications.

The last four chapters are a more mixed collection. Winget wrestles with the old problem of indices that can be designed to integrate physical, chemical, and biological data, one that goes back to the beginning of the century and the old German Saprobiensystem. He comes down heavily in favour of one that he designed himself, but which, perhaps significantly, has been published only in a United States Department of Agriculture document in 1979. Personally, I always regard any such index with suspicion, and I wonder why we have to bother to quantify the essentially unquantifiable. It is often said that it is in order to satisfy engineers, who like to deal with numbers, or bureaucrats, who are too lazy or ignorant to try to work without them. But we do not demand that our medical practitioners quantify their diagnoses, and even engineers have to put up with professional judgements about their own health. Indeed, I would hope that they would see it as ludicrous to expect numbers in such situations, and the environment is not any more quantifiable. I therefore found this chapter rather out of place.

Starnes gives a good account of the effects of coal mining in the eastern states, pointing out how devastated areas recover in time, and how this process can be aided by construction. I found this case-by-case study very interesting, but I was irritated by the general scruffiness of some of the figures. There follows a chapter by Burgess, who examined in some detail the effects of various stream-improvement constructions on the production of brook trout in a stream in Quebec, a practical demonstration of the benefits to be derived from the activities recommended by Wesche. This stream had been divided so that it provided a control as well as an experimental reach, and it is interesting that the changes that had benefitted the fishes had also increased the standing stock of crayfish.

The final chapter, by Judy, I found the least satisfactory among the nine that constitute the book. It deals with the chemistry of runoff from the urban area of Denver, Colorado, but I found it very uninformative, and I wonder why it was included, as it reaches no firm conclusion and does not really deal with restoration. Or maybe it is just that I found it very hard to read. The map that explains the sampling program is almost impossible to understand, chiefly, I think, because the river has been left out, and the text is full of acronyms which the reader forgets between pages.

So we have here a book that has much of interest, and which, despite some faults and limitations, acquaints the reader with

the contents and philosophy of some rather obscure official United States publications; but whether it is worth $40 is a matter of opinion. On the whole it has been well proofread, and I suppose that one must forgive Americans for their misuse of the word "watershed." However, I remain critical of such gems as "right of ways" and "as best as possible", and why do so many educated people not know that "criteria" has a singular, and that "methodology" does not mean "method"?

H. B. N. HYNES

Department of Biology
University of Waterloo
Waterloo, Ont. N2L 3G1

(R657)

BOOKS RECEIVED / LIVRES REÇUS

Erie: the lake that survived. *Noel M. Burns. Rowman and Allanheld, Totowa, NJ. 1985. 320 p. $34.95 (U.S.). ISBN 0-8476-7398-7.* The impact of man's presence on the lake from precolonial times to the present is traced. The environmental degradation and hard-fought partial restoration of the severely stressed ecosystem are documented. The cause and effect relationships are drawn in a quantitative manner. [R693]

Tidal flat ecology: an experimental approach to species interactions. Ecological Studies 54. *Karsten Reise. Springer-Verlag New York Inc., New York, NY. 1985. 191 p. $34.50 (U.S.) ISBN 3-540-15447-7, ISBN 0-387-15447-7.* The focus of this book is on the field experiments carried out to determine the role of species interactions in shaping the tidal flat communities. It is based on 10 yr of experimental experience with mud, sand, and worms in the European Wadden Sea and will be the basis for more comprehensive research on the tidal flat ecotone. [R694]

Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes. *F. Bookstein, B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss (editors). Special Publication 15, The Academy of Natural Sciences of Philadelphia, Philadelphia, PA. 1985. 277 p. ISBN 0-910006-47-4 (hardcover), ISBN 0-910006-48-2 (softcover).* This text is suitable for those with a working knowledge of biological statistics. It gives a general approach to morphometrics, the study of biological questions using geometric information, with new models and refinements of older methods. Helpful tools are introduced for use of computers in selecting, acquiring, transforming, and analyzing data from biological shapes. [R695]

Artificial seawaters: formulas and methods. *Joseph P. Bidwell and Stephen Spotte. Jones and Bartlett Publishers, Inc., Boston, MA. 1958. 349 p. ISBN 0-86720-057-X.* This book gives 169 recipes of seawater substitutes devised at one time or another for different purposes. Because enrichments are trace solutions incapable by themselves of supporting life, they have been largely ignored. The formulae are in a standard format and should provide useful tools for professionals. [R696]

Exploitation of marine communities. *R. M. May (editor). Life Sciences Research Report 32. Report of the Dahlem Workshop on Exploitation of Marine Communities, Berlin 1984, April 1–6. Springer-Verlag New York Inc., New York, NY. 1985. 366 p. $20.00 (U.S.) ISBN 3-540-15028-5, ISBN 0-387-15028-5.* The goal of the Dahlen Workshop was to evaluate the ability of fishery science and management to deal with changes in the marine ecosystems. The themes were dynamics of single populations, dynamics of systems with many species, management under uncertainty, and multispecies management. [R697]

Engineering approaches for lake management. Volume 1: Data analysis of empirical modeling. *Kenneth H. Reckhow and Steven C. Chapra. Butterworth Publishers, Boston, MA. 1985. 320 p. $85.00 (U.S.) set. ISBN 0-250-40344-7.* This volume introduces a variety of statistical methods and empirical models. It examines some common problems in lake water quality assessment and evaluates statistical methods useful for problem solution. It treats effective modeling based on a sound observational program, techniques for the estimation of uncertainty, and simplicity in lake modeling. [R698]

Engineering approaches for lake management. Volume 2: Mechanistic modeling. *Steven C. Chapra and Kenneth H. Reckhow. Butterworth Publishers, Boston, MA. 1985. 492 p. $85.00 (U.S.) set. ISBN 0-250–40392-7.* This volume provides an in-depth analysis and integration of the various processes pertaining to a single system. It is designed as a starting point for those wishing to gain proficiency in the art of water quality analysis. Descriptions and examples that elucidate the fundamental concepts that underlie most concepts are included. [R699]

Fish endocrinology. *A. J. Matty. Timber Press, Portland, OR. 1985. 267 p. $27.95 (U.S.). ISBN 0-88192-024-X.* This book aims to place fish endocrinology within the context of comparative anatomy and physiology. It discusses the evolution of hormones and applied aspects and synthesizes what is currently known about fish hormones. It also serves as a handbook for those using hormones in managing fish populations. [R700]

Recent advances in aquaculture. *James F. Muir and Ronald J. Roberts (editors). Westview Press, Boulder, CO. 1985. 453 p. $42.00 (U.S.). ISBN 0-86531-464-0.* This book aims to fill the gap between current research and the needs of aquaculturists, teachers, and planners. It includes sections on fisheries and aquaculture significance of mangrove swamps, farming crustaceans in western temperate regions, snakeheads, carp nutrition, tilapia culture, and recirculated water systems. [R701]

Biology of the arctic charr: Proceedings of the international symposium on arctic charr. *Lionel Johnson and Bonnie Burns (editors). University of Manitoba Press, Winnipeg, Man. 1985. 584 p. $60.00. ISBN 0–88755-137-8.* The symposium, held in 1981, brought together researchers, managers, processors, and those dependent on the stocks for part of their livelihood. It is a unique compendium on a single species and includes aspects of taxonomy, physiology, population dynamics, parasitology, and utilization. [R702]

ANNOUNCEMENTS / AVIS

International Conference on Fisheries (Quebec, Canada)

An international conference on Fisheries and Economic Development will be held at the University of Quebec at Rimouski (Canada) from 10 to 15 August 1986. It is being sponsored jointly by the Marine Resources Study Group at the University of Quebec and by the International Institute of Fisheries Economics Trade (Oregon State University, Corvallis, Oregon).

Proposed topics include national economic objectives, the alternatives, the difficulties, and the consequences of public intervention in the fishery sector, and exports and their effect on developing countries. Areas of research ranging from fishing methods and the effectiveness of different types of boats and gear to policies regulating a fishery, from the modernization of the fleet to limits on fishing zones and seasons, and from the protection of stocks to training program for fishery managers will be treated.

For further information please contact Mr. Pandelis Vlahopoulos, Conference Coordinator, Marine Resources Study Group, Universite du Quebec a Rimouski, 300 avenue des Ursulines, Rimouski (Quebec), Canada G5L 3A1. Telephone: (418) 724-1576.

Second International Colloquium on Pathology in Marine Aquaculture (2nd PAMAQ)

The meetings will be held from 7 to 11 September 1986 at Porto, Portugal. The subjects to be covered are virosis; bacteriosis; mycosis and protozoosis of crustacea, Mollusca, fishes, and other animal groups; nutrition; and quality of water.

For further information pleast contact Carlos Azevedo, President of the Organizing Committee, 2nd PAMAQ, Department of Cell Biology, Institute of Oporto, 4000 Porto, Portugal.

Conférence internationale sur les pêches (Québec, Canada)

Une conférence internationale sur les pêches et le développement économique aura lieu à l'université du Québec à Rimouski (Canada) du 10 au 15 août 1986. Elle sera parrainée conjointement par le groupe d'étude sur les ressources marines de l'Université du Québec et par l'International Institute of Fisheries Economics Trade (Université de l'État de l'Orégon, Corvallis, Oregon).

Les sujets proposés comprennent les objectifs économiques nationaux, les solutions de rechange, les difficultés et les conséquences de l'intervention du public dans le secteur des pêches, de même que les exportations et leurs effets sur les pays en voie de développement. On y traitera de domaines de recherche allant des méthodes de pêche et de l'efficacité de divers types de bateaux et d'engins aux politiques régissant une pêche donnée, de la modernisation de la flottille aux limites visant les zones et les saisons de pêche, et de la protection des stocks au programme de formation à l'intention des gestionnaires des pêches.

Pour de plus amples informations, veuillez communiquer avec M. Pandelis Vlahopoulos, coordonnateur de la conférence, Groupe d'étude sur les ressources marines, Université du Québec à Rimouski, 300, avenue des Ursulines, Rimouski (Québec), Canada G5L 3A1. Téléphone : (418) 724−1576.

Deuxième colloque international sur la pathologie en aquiculture marine (2ième PAMAQ)

Les réunions auront lieu à Porto, au Portugal, du 7 au 11 septembre 1986. Les sujets traités seront la virose; la bactériose; la mycose et la protozoose chez les crustacés, les mollusques, les poissons et d'autres groupes d'animaux; de même que la nutrition; et la qualité de l'eau.

Pour de plus amples informations, veuillez communiquer avec Carlos Azevedo, Président du comité d'organisation, 2ième PAMAQ, Département de biologie cellulaire, Institut d'Oporto, 4000 Porto, Portugal.

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTS PUBLICATIONS

VOLUME 42, No. 4 — article by P. A. Chambers and J. Kalff: *Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth.*

Page 701, abstract line 6: "1 cal/cm^2 = 0.239 J/cm^2" should read "1 J/cm^2 = 0.239 cal/cm^2."

Page 705: Irradiance values in Tables 2 and 3 and in the text must be multiplied by 17.5 to give the correct value in J/cm^2.

VOLUME 42, No. 7 — article by T. G. Smith, M. O. Hammill, D. J. Burrage, and G. A. Sleno: *Distribution and abundance of belugas,* Delphinapterus leucas, *and narwhals,* Monodon monoceros, *in the Canadian high Arctic.*

Pages 678–679, Fig. 2: first line of the caption should read "Location of strata, transects, and sightings of belugas and narwhals during the (a) August 1981 and (b) July 1981 strip transect aerial surveys."

VOLUME 42, No. 10 — note by R. K. Misra: *Quadratic discriminant analysis with covariance for stock delineation and population differentiation: a study of beaked redfishes* (Sebastes mentella *and* S. fasciatus).

Dr. R. R. Rawlings confirmed and agreed to correct prior to publication an error in R. R. Rawlings, B. I. Graubard, S. Teper, R. S. Ryback, and M. J. Eckardt (1985. Conditional quadratic discrimination in the identification of biological markers for disease screening. Biom. J. (In press)). Subsequently, the following corrections were made in Misra (1985) and redfish data reanalyzed:

Page 1674, below QDF equation: α_i for $i = 1, 2$ should read "$\alpha_i = \mu_{x_i} + A_{xz_i} \cdot A_{zz_i}^{-1} (z - \mu_{z_i})$."

Page 1676, left column: lines 8–11 should read "The leave-one-out estimator identified a total of 6 misclassified individuals, which included 3 individuals from each sample, out of a total of 198. The estimated expected error rate was thus 3%."

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Articles

Model for streamwater chemistry of a tributary to Harp Lake, Ontario
S. Rustad, N. Christophersen, H. M. Seip, and P. J. Dillon

Stunted lake trout (*Salvelinus namaycush*) from the Rocky Mountains **D. B. Donald and D. J. Alger**

Further analysis of population trends in the northwest Atlantic harp seal (*Phoca groenlandica*) from 1967 to 1985 **D. Roff and W. D. Bowen**

Free amino acid pools of five species of freshwater oligochaetes
R. L. Graney, T. J. Keilty, and J. P. Geisy

Quantifying changes in British Columbia Dungeness crab (*Cancer magister*) landings using intervention analysis **D. Noakes**

Toxicity of trace metal mixtures to American flagfish (*Jordanella floridae*) in soft, acidic water and implications for cultural acidification **N. J. Hutchinson and J. B. Sprague**

Natural and acquired agglutinins to *Aeromonas hydrophila* in carp (*Cyprinus carpio*)
C. H. J. Lamers and W. B. Van Muiswinkel

Significance of cannibalism in larval walleye (*Stizostedion vitreum*)
N. L. Loadman, G. E. E. Moodie, and J. A. Mathias

Fidelity of American shad, *Alosa sapidissima* (Clupeidae), to its river of previous spawning
G. D. Melvin, M. J. Dadswell, and J. D. Martin

Growth of *Lampsilis radiata* (Bivalvia: Unionidae) in sand and mud: a reciprocal transplant experiment
S. G. Hinch, R. C. Bailey, and R. H. Green

Current response and agonistic behavior in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations **E. B. Taylor and P. A. Larkin**

Internal phosphorus load in an oligotrophic Precambrian Shield lake with an anoxic hypolimnion
G. K. Nürnberg, P. J. Dillon, and D. J. McQueen

Salmonid whirling disease: dynamics of experimental production of the infective stage — the triactinomyxon spore **M. E. Markiw**

Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area **T. E. Nickelson**

Background levels of petroleum residues in the waters and surficial bottom sediments of the Labrador shelf and Hudson Strait/Foxe Basin regions **E. M. Levy**

Size selectivity of coho (*Oncorhynchus kisutch*) preying on juvenile chum salmon (*O. keta*)
N. B. Hargreaves and R. J. LeBrasseur

Distribution and association of larval crabs (Decapoda: Brachyura) on the Scotian Shelf
J. C. Roff, L. P. Fanning, and A. B. Stasko

Temperature-sensitive period of sex determination in the Atlantic silverside, *Menidia menidia*
D. O. Conover and M. H. Fleisher

Comparison of methods for estimating annual productivity of the copepods *Acartia hudsonica* and *Eurytemora herdmani* in Passamaquoddy Bay, New Brunswick **K. Middlebrook and J. C. Roff**

Zooplankton community and species responses to a natural turbidity gradient in Lake Temiskaming, Ontario–Quebec **E. R. Zettler and J. C. H. Carter**

Analysing the effect of age structure on stock–recruitment relationships in herring (*Clupea harengus*)
A. A. Rosenberg and R. W. Doyle

Effects of pH changes on zinc uptake by *Chlamydomonas variabilis* grown in batch culture
G. I. Harrison, P. G. C. Campbell, and A. Tessier

Colonization of natural substrates by stream benthos **B. L. Peckarsky**

Parr–smolt transformation in female and sexually mature male anadromous and nonanadromous Atlantic salmon, *Salmo salar* **T. P. Birt and J. M. Green**

Direct and indirect effects of arsenic on the survival and fecundity of estuarine zooplankton
J. G. Sanders

Notes

Ecophysiology and mercury accumulation of rainbow trout (*Salmo gairdneri*) when exposed to mercury in various concentrations of chloride **B. Z. Walczak, U. T. Hammer, and P. M. Huang**

Interrenal, thyroidal, carbohydrate, and electrolyte responses in rainbow trout (*Salmo gairdneri*) during recovery from the effects of acidification **S. B. Brown, R. E. Evans, and T. J. Hara**

Use of calcareous otic elements (statoliths) to determine age of sea lamprey ammocoetes (*Petromyzon marinus*) **E. C. Volk**

Book reviews / Comptes rendus

Environmental impacts of smelters. Advances in environmental science and technology. Vol. 15 (edited by J. O. Nriagu) **J. F. Klaverkamp**

Bioeconomic modelling and fisheries management (C. W. Clark) **G. T. Evans**

Diseases of marine animals: introduction to Volume IV, Part II: Pisces (edited by O. Kinne) **C. M. Morrison**

Fishes of the world. 2nd edition (Joseph S. Nelson) **C. C. Lindsey**

Books received/Livres reçus

Announcements/Avis

Limnetic zooplankton assemblages in Atlantic Canada with special reference to acidification J. H. C. Carter, W. D. Taylor, R. Chengalath, and D. A. Scruton **444–456**

Effects of density-dependent and climatic factors on American shad, *Alosa sapidissima*, recruitment: a predictive approach V. Crecco, T. Savoy, and W. Whitworth **457–463**

Reviews / Synthèses

El Niño, interannual variability and fisheries in the northeast Pacific Ocean L. A. Mysak **464–497**

Notes

Possible effects of the Sitka eddy on sockeye (*Oncorhynchus nerka*) and pink salmon (*Oncorphynchus gorbuscha*) migration off southeast Alaska K. Hamilton and L. A. Mysak **498–504**

Book reviews / Comptes rendus

The restoration of rivers and streams: theories and experience (edited by James A. Gore) H. B. N. Hynes **505–506**

Books received / Livres reçus **507**
Announcements / Avis **508**
Corrections to recent publications / Corrections sur récents publications **509**
Coming next month / À paraître le mois prochain **510–511**

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 43, No. 2, February 1986 — Volume 43, n° 2, février 1986

Articles

Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia T. D. Beacham and C. B. Murray 252–262
Winter survival and growth of *Chondrus crispus* in onshore culture tanks P. F. Shacklock and J. S. Craigie 263–268
Environmental and parental influences on age at maturity in sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia R. M. Peterman, M. J. Bradford, and J. L. Anderson 269–274
Effects of chronic exposure to sublethal pH on growth, egg production, and ovulation in brook trout, *Salvelinus fontinalis* W. H. Tam and P. D. Payson 275–280
Changes in mean weight, sea-age composition, and catch-per-unit-effort of Atlantic salmon (*Salmo salar*) angled in the Godbout River, Quebec, 1859–1983 A. T. Bielak and G. Power 281–287
Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca* M. Stephenson and G. L. Mackie 288–292
Introduction: Phosphorus–Plankton Dynamics Symposium S. J. Tarapchak and C. Nalewajko 293–301
Epilimnetic phosphorus cycling: influence of humic materials and iron on coexisting major mechanisms D. A. Francko 302–310
Does algal–bacterial phosphorus partitioning vary among lakes? A comparative study of orthophosphate uptake and alkaline phosphatase activity in freshwater D. J. Currie, E. Bentzen, and J. Kalff 311–318
Phosphate uptake by microorganisms in lake water: deviations from simple Michaelis–Menten kinetics S. J. Tarapchak and L. R. Herche 319–328
Light history, phosphorus status, and the occurrence of light stimulation or inhibition of phosphate uptake in Lake Superior phytoplankton and bacteria C. Nalewajko, B. Paul, K. Lee, and H. Shear 329–335
Microbial recycling of phytoplankton phosphorus J. V. De Pinto, T. C. Young, J. S. Bonner, and P. W. Rodgers 336–342
Dissolved organic phosphorus compounds: do they satisfy planktonic phosphate demand in summer? R. T. Heath 343–350
Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si:P loading gradient S. S. Kilham 351–360
Phosphorus regeneration by the predatory copepod *Diacyclops thomasi* J. A. Bowers 361–365
A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227, northwestern Ontario S. N. Levine, M. P. Stainton, and D. W. Schindler 366–378
Identification of critical nutrient levels through field verification of models for phosphorus and phytoplankton growth M. T. Auer, M. S. Kieser, and R. P. Canale 379–388
Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition E. Sakshaug and Y. Olsen 389–396
Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures C. F. D'Elia, J. G. Sanders, and W. R. Boynton 397–406
Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes C. L. Schelske, E. F. Stoermer, G. L. Fahnenstiel, and M. Haibach 407–415
Synopsis: Phosphorus–Plankton Dynamics Symposium S. J. Tarapchak and C. Nalewajko 416–419
Zooplankton species abundance and biomass in relation to occurrence of *Mysis relicta* (Malacostraca: Mysidacea) R. W. Nero and W. G. Sprules 420–434
Influence of salmonid predation and weather on long-term water quality trends in Lake Michigan D. Scavia, G. L. Fahnenstiel, M. S. Evans, D. J. Jude, and J. T. Lehman 435–443

(*continued inside back*)

©Minister of Supply and Services Canada 1986
Ministre des Approvisionnements et Services Canada 1986

CJFSDX43(2) 251–511 (1986)
ISSN 0706-652X

Subscription rates / Abonnements

Canada: Institutional / Collectif $150; Personal / Personnel $50
Other countries / Autres pays: Institutional / Collectif $180; Personal / Personnel $60
Single issue / Par numéro: $11.95 (Canada); $14.35 (Other countries / Autres pays)